COTTON INSECTS AND MITES:

Characterization and Management

NUMBER THREE
THE COTTON FOUNDATION
REFERENCE BOOK SERIES

Edited by
Edgar G. King,
Jacob R. Phillips
and
Randy J. Coleman

COTTON INSECTS AND MITES:
Characterization and Management

THE COTTON FOUNDATION

Reference Book Series

The Cotton Foundation was created in 1955 to foster research and education for the cotton industry. Supported by membership dues and grants from agribusiness firms, the Foundation plays an integral role in focusing attention to high priority needs. Foundation members include the world's finest manufacturers and suppliers of cotton machinery, plant health products, planting seed, testing instruments, processing materials and consulting, financial and communications services.

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We are pleased to publish **COTTON INSECTS AND MITES: Characterization and Management,** the third in the series of cotton reference books. The first volume, **COTTON PHYSIOLOGY** was published in 1986, the second, **WEEDS OF COTTON: Characterization and Control** was published in 1992 and the fourth volume, **VEGETABLE OILS AND AGRICHEMICALS** became available in 1994.

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Bayer's Agriculture Division is part of the worldwide network of Bayer group organizations. Through the expertise of the worldwide Bayer Group, Bayer has been able to bring to the U. S. innovative products for the cotton industry for over forty years.

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Bayer's Agriculture Division is proud to be a member and participant in the activities of The Cotton Foundation. The sponsorship of **COTTON INSECTS AND MITES: Characterization and Management,** the third book in the Foundation's cotton reference book series, provides us the opportunity to extend to the industry the latest technical information concerning pest management and to supply information needed for the development of a stronger, more profitable cotton industry.

COTTON INSECTS AND MITES: Characterization and Management

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TABLE OF CONTENTS

SECTION II

TECHNOLOGICAL COMPONENTS OF INSECT AND MITE MANAGEMENT

SECTION III

SUPPRESSION COMPONENTS

SECTION VI

ECONOMICS OF INSECT AND MITE PEST CONTROL

SECTION VII

PERSPECTIVES

FOREWORD

To appreciate the impact of insect and mite pests on cotton production one needs to consider the cotton plant itself and the environment and conditions under which it is grown. For in-depth knowledge of the cotton plant—its botanical, physiological, and reproductive, etc. characteristics—the reader is referred to **COTTON PHYSIOLOGY**, Number 1 in The Cotton Foundation Reference Book Series.

Commercial production of cotton in the United States and most production areas of the World is as an annual crop with each season starting from planting the seed and ending with harvest. This is true even though the cotton plant botanically is a perennial.

In commercial production of cotton, the balance between vegetative and fruiting development at most stages throughout the growing season is critical to successful production. Among the major categories of stress factors that influence this balance is insect and mite pests.

There are hundreds of insect and mite species that are potential cotton pests. However, as recognized by professional cotton entomologists and producers, the major economic cotton insect and mite pests in the United States are considered in twenty one groups, some groups consisting of more than one species.

This book on **COTTON INSECTS AND MITES** was conceived in 1985 as a joint project of the annual Cotton Insect Research and Control Conference and The Cotton Foundation. A proposed contents outline for the Book was submitted to a distinguished Advisory Committee to help formulate its contents; the project was officially begun in 1987. Advisory Committee members, classified by their 1986 positions, were Perry L. Adkisson, Deputy Chancellor, Texas A&M University, College Station, TX; T. Don Canerday, Chairman, Division of Economic Entomology, University of Georgia, Athens, GA; Robroy Fisher, Cotton Producer, Glen Allan, MS; T. J. Henneberry, Director, Western Cotton Research Laboratory, U. S. Department of Agriculture, Agricultural Research Service, Phoenix, AZ; Louise Henry, Co-Owner, Henry Agri-Scientific, Bishop, GA; Harry L. McMenemy, Regional Technical Manager, Agricultural Division, Mobay Chemical Corporation, Memphis, TN; Leon Moore, Extension Entomologist, Cooperative Extension Service, University of Arizona, Tucson, AZ; H. T. Reynolds, University of California (Retired), Riverside, CA; and Ronald H. Smith, Extension Entomologist, Cooperative Extension Service, Auburn University, Auburn University, AL.

In an early stage of its development, **COTTON INSECTS AND MITES** was designated as Number 3 in the Cotton Foundation Reference Book Series. Number 1, **COTTON PHYSIOLOGY**, was already published (1986), and Number 2, **WEEDS OF COTTON** (1992) was much further advanced in development at that time. As it turned out, Number 4, **VEGETABLE OILS AND AGRICHEMICALS**, was developed much faster and was published in 1994 ahead of **COTTON INSECTS AND MITES**. Factors contributing to this were the much more extensive and comprehensive treatment of the subject and the involvement of a much larger

number of authors with COTTON INSECTS AND MITES.

I have had the pleasure of serving as executive editor and publishing coordinator for all four of these cotton reference books. My work has been mainly with the editors and the printing companies. The editors, in working with the authors, have done most of the work. In the case of **COTTON INSECTS AND MITES**, this has meant working on thirty chapters involving eighty contributors.

Drs. Edgar G. King and Jacob R. Phillips were selected originally by their peers to edit this book. Both have had distinguished and fruitful careers as cotton research entomologists. Dr. Phillips was recipient of the prestigious Mobay Cotton Research Recognition Award for 1990. This award program was administered by The Cotton Foundation. In 1993 Dr. King was recognized with the Outstanding Scientist of the Year Award presented by the Agricultural Research Service of the U. S. Department of Agriculture. Dr. Phillips retired from the University of Arkansas before publication of this book was completed. Dr. King still serves as a researcher and research administrator with USDA's Agricultural Research Service.

Mr. Randy J. Coleman, a co-worker of Dr. King, became heavily involved in editing soon after this book was started. He became a major contributor to its development. The addition of Mr. Coleman as one of the editors is most deservingly in recognition of his dedicated efforts and many contributions.

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PREFACE

The book **COTTON INSECTS AND MITES: Characterization and Management** is the most comprehensive review and synthesis of knowledge and technology on United States cotton insects and mites available today. The book includes an introductory Commemoration" reviewing the fifty-year history of the Cotton Insect Research and Control Conference followed by 30 chapters. Chapter 1, "Major Developments in Management of Insect and Mite Pests in Cotton," summarizes key events leading to the state-of-the-art for managing insect and mite pests in cotton. The other 29 chapters are divided into seven sections [Section I "Characterization of Insect and Mites" (four chapters); Section II "Technological Components of Insect and Mite Management" (seven chapters); Section III "Suppression Components" (five chapters); Section IV "Concepts of Population Management" (two chapters); Section V "Implementation of Insect and Mite Pest Management Programs" (four chapters); Section VI "Economics of Insect and Mite Pest Control" (three chapters); and Section VII "Perspectives" (four chapters)].

The concept of publishing a book on "Cotton Insects and Mites..." to commemorate and complement the Cotton Insect Research and Control Conference was first conceived in 1985. The intent was to update and expand the control, biological, and survey information heretofore given in pre-1985 Conference reports, as well as to synthesize information for cotton entomology in the United States. An expectation was to publish a book on cotton insects and mites that would be useful to growers as well as the scientific and technological community. Our hope is that this book will serve as a springboard for improved management of cotton insects and mites.

Eighty of the United States leading authorities on "Cotton Insects and Mites" contributed to the development of this book. It reflects pioneering research conducted by hundreds of scientists, the rich history of the cotton industry, the efforts of extension personnel, economists, and consultants to communicate and transfer the technologies, and the indomitable spirit of cotton growers, who each year must produce a profitable crop despite competition by insects and mites and other pests for the seed and fiber. This book, reflecting the extraordinary complexity of the interactions between the plant, insects and mites, and the cotton production and utilization community, truly was an interdisciplinary accomplishment involving the public and private sector. Consequently, it is not surprising that it cites 3200 references and is over 1000 pages in length.

These contributions summarize and synthesize knowledge by many of the United States most recognized cotton insect and mite authorities. And, in some cases, they are among their last major scientific contributions. One scientist, C. A. (Mr. Charlie) Parencia, lead author of the "Commemorative" paper and chronicler of the Cotton Insect Research and Control Conference for sixteen years and a participant for 35 of its 50-year existence passed away in 1987. One of the United States most eminent authorities on the "Biology and Ecology of Important Insect and Mite Pests of Cotton," (Chapter 2), T. F. (Tom) Leigh, passed away in 1993. Other chapters were

coauthored by authorities who have since retired, but many have continued their work in other roles within the cotton industry. On the other hand, the search for new information, new and improved technology, and the communication and transfer of this information and technology is being continued by a new generation of research scientists, extension entomologists, and consultants as exemplified in their contributions to this book.

The cotton field is home for hundreds of insect and mite species, but only a relatively few actually can be termed pests, i.e., competitors with people for seed and fiber. Most of the organisms inhabiting these fields are, in fact, beneficial, either as predators or parasites of potential pests or serving as food for the predators and parasites. Many microbials, including viruses, bacteria, fungi, microsporidia, and nematodes also function as beneficials attacking potential pests. Nevertheless, according to the 1996 Cotton Insect Research and Control Conference Proceedings, estimated management costs and revenue losses to insect and mite pests in 1995 were $1.68 billion, despite the application of insecticides and miticides.

As stated by Dr. J. R. Bradley in Chapter 1, "The entry of the boll weevil into the United States [in 1892] is probably the single most important entomological event to have occurred in cotton." It was largely responsible for the shift of cotton production from the Southeast to the Southwest. Efforts to control this exotic pest that arrived without a complement of co-evolved natural enemies has driven cotton insect and mite management practices for over 100 years. The pink bollworm is a similar force in the Far West and plant bugs often serve as key pests in the Mid-South. These insects are often labeled as key pests because they are not effectively controlled by natural enemies and consequently each growing season they are among the first pests requiring insecticide application.

The evolution of plant insect and mite management practices and the use of synthetic chemical pesticides in cotton often has been in the forefront of technological developments in plant entomology in the United States. The development of short-season cotton varieties and stalk destruction was initiated to avoid late-season damage by boll weevil and bollworm populations. The cotton industry began using arsenicals to control the boll weevil in the 1920s, and cotton was one of the first crops where pesticides were applied aerially. Synthetic organic insecticides have been used extensively since their discovery in the 1940s. However, resistance to these chemicals quickly evolved with the occurrence of organochlorine resistance in the boll weevil in 1955 and shortly thereafter in the bollworm and tobacco budworm to organochlorines and organophosphate compounds. The trend of introduction of new chemicals, development of resistant insect and mite populations, outbreaks of secondary pests (often as a consequence of the elimination of natural enemies), and the research and development of new chemicals to manage the ever evolving complex of insect and mite pests is a constant challenge to the grower, industry, and researchers to evolve new and improved control technologies.

The National Cotton Council of America recognized the futility of this treadmill of discovery, obsolescence, and increasing cost and complexity and the key role of

the boll weevil as a pest in the Southeast, Mid-South, and Southwest in this evolutionary sequence. They enlisted the support of the federal, state, and private sector as early as 1957 in their efforts to eradicate the boll weevil from the United States. The successful elimination of the boll weevil as a pest of cotton in Virginia, the Carolinas, Georgia, north Florida, California and Arizona is a major entomological success story, rivaling the successful eradication of the screwworm from North America. Nevertheless, elimination of the boll weevil from the Mid-South and Southwest has been more intractable and the search continues for new and improved technologies to aid efforts in eliminating the weevil as a pest in the rest of the United States and northern Mexico. The evolution of these efforts is detailed in Chapter 19.

COTTON INSECTS AND MITES: Characterization and Management establishes a foundation on the biology, ecology, and systematics of pests and their natural enemies, discusses technological tools for managing pests and their natural enemies, reviews field-by-field and population management tactics, and integrates this information into implementation programs for four broadly defined production regions of the United States. Extension entomologists collaborated in authoring the chapter for their respective region. The economics of these pest suppression and elimination strategies are discussed and placed in context with environmental issues and the cotton production and utilization community. The interaction between the grower, research, extension, and consultant communities was of particular interest.

The 1989 Entomological Society of America "Common Name of Insects and Related Organisms" was the guide for species nomenclature used in this book. Accordingly, the scientific names *Helicoverpa zea* and *Heliothis virescens* refer to the bollworm and the tobacco budworm, respectively, thereby acknowledging that these two pests differ considerably and are not collectively "heliothis" or "bollworms." Another potential area of confusion involved the common term "plant bugs" to describe several genera of bugs in the family Miridae. The genus *Lygus* contains several species, and one in particular, *Lygus hesperus* has no approved common name, however, it is referred to as the western lygus bug throughout the monograph. Recently, differences in enzyme patterns, biology, extended host range, crossing experiments, and mating behavior observations within populations of the sweetpotato whitefly, *Bemisia tabaci*, have indicated that strains or biotypes exist for this species. Perring *et al.* (1993) suggested that the sweetpotato whitefly strain B is truly a distinct species and named it the silverleaf whitefly, *Bemisia argentifolii*. Where appropriate, this terminology has been adopted in discussing this organism.

We express our appreciation to the many authors who contributed their time to make this book possible, to the Bayer Corporation, Agriculture Division for support in publication of the book, and to The Cotton Foundation and the National Cotton Council of America for their leadership and support throughout the development and completion of the book. Dr. James M. Brown, in his role as consultant to The Cotton Foundation, deserves a special thanks for facilitating completion of this book and in maintaining the continuity of The Cotton Foundation Reference Book Series.

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COMMEMORATION

The monograph COTTON INSECTS AND MITES: Characterization and Management would not be complete without a brief historical review of the Cotton Insect Research and Control Conference. The Conference has been held annually since its beginning in 1947. This monograph has been written in commemoration of the conference.

Each year cotton research and extension entomologists from sixteen cotton growing State Agricultural Experiment Stations, the United States Department of Agriculture, the National Cotton Council of America, Cotton Incorporated, consultant organizations, and the chemical industry meet to review research and experiences of the current year. Special topics such as insecticide resistance are often treated to develop guidelines for the upcoming year.

The Conference was initiated on November 17-19, 1947 and brought to fruition the desire of the late R. W. Harned (Chief of Cotton Insect Research for the U. S. Department of Agriculture from 1931 to 1953) to develop a conference for fostering cooperation and understanding among cotton entomologists. The advent of the synthetic organic insecticides, which were so much more effective than those previously available, generated a favorable climate for the conference; rapid evaluation of the new materials was imperative.

Fifty-two conferees attended the first conference with the number escalating to well over several hundred in subsequent years. The annual report of the conference came to be known as the cotton insect bible of the world, and it was distributed throughout the world wherever cotton was grown. So, R. W. Harned may be considered to be the Father of the conference.

The first five conferences did not include representatives from states where cotton was irrigated, viz. New Mexico, Arizona and California. However, the head of the Agriculture Research Agency (ARA) Laboratory, U. S. Department of Agriculture, Tucson, Arizona sat in on one of the conferences as an observer. Thereafter, representatives from all cotton growing states and Puerto Rico (for some years) participated in the conference.

The Agricultural Research Service (ARS) and its predecessor, ARA, have, in the past, had major responsibility for the management and coordination of the conference. R. W. Harned served as Chairman for the first six conferences, K. P. Ewing for the next four, C. F. Rainwater for the next eight, and C. R. Parencia, who participated in the first thirty-five conferences, for the next sixteen. With the latter's retirement, J. R. Phillips (University of Arkansas) and M. E. Merkl (ARS) became Co-Chairmen for the 35th and subsequent conferences with the former responsible for the conference and the latter for revision, publication and distribution of the report. Phillips was replaced by G. A. Herzog (University of Georgia) after the 42nd Conference, and when Merkl retired after the 36th Conference, he was replaced by D. L. Bull (ARS) who left cotton insects after the 38th Conference. Bull was replaced by E. G. King (ARS) for the 39th-43rd, and D. D. Hardee (ARS) succeeded King. As of the 46th Conference, Herzog and Hardee are Co-Chairmen.

Initially, the Conference was conducted over a three-day period with detailed reports being presented by research and extension personnel from each of the states. More recently, this time has been reduced to two days with the first half day being occupied by symposia on selected topics and the subsequent one and one-half days devoted to contributed papers and a business meeting.

R. W. Harned, the first Conference Chairman, called time on no one. Consequently, discussions were often prolonged. Then, too, the early reports of the conferences were written and revised during the conferences. In retrospect, valuable time was expanded over the choice of a word or the efficacy of a compound at a certain dose against an insect. Regardless, Professor Harned wanted a unanimous decision.

The success of the conferences depended on the airing of all views. Under Professor Harned's patient guidance, a diverse group of strong-willed, independent professionals joined together for the common good. It took time and sometimes the issue, unresolved, was tabled until the following year. Professional convictions and personal feelings were kept apart and insults were rare, although tempers often flared. Once the dust had settled, conferees were friends and fellow professionals, not adversaries. As time progressed, timing of discussion was expedited.

In the early years it was the policy of conferees to meet in closed sessions excluding members from the chemical industry because new materials were coming into the picture rapidly and conferees felt that full and complete discussions of their efficacy could be held in no other way. As it was, participants exceeded desirable numbers, and addition of other personnel, especially those interested in promotion, could result in chaos. A concession to alleviate the exclusion was made in that once the insecticide efficacy section of the annual report was approved, it would be mimeographed and distributed to attendees of the subsequent Beltwide Cotton Production Conference. Distribution of this section took precedence over the regular program. It was anxiously awaited by farmers and ginners as much as by representatives of chemical companies. Members of industry thus did not have to wait until the report was published to receive the information; this was an important consideration when one realized that the future of a new insecticide might be affected by the conference report.

The first several conferences included detailed oral reporting of research results and experiences of conferees. In addition, copies of research results of a laboratory or experiences of extension personnel were brought to the conference for distribution. Data often were confidential, which was another reason for closed sessions. Although the chemical industry supported open sessions, it did not want data relating to certain compounds to be released until it was ready to release their chemistry. The policy was established that no compound was to be listed in the annual report until its chemistry was removed from the confidential status list.

Procedures for revising the Conference Report were changed in 1960 in preparation for the 14th Annual Conference on Cotton Insect Research and Control resulting in less time being needed to consider and adopt the report at the conference. Thus, one of the half-day sessions was devoted to current topics of interest presented by invited speakers. This usually was on the last one-half day of the conference. This session of

the 18th conference (1965) was not billed as an open session but word was passed that the general public was welcome to attend. This session has been open to general attendance since that time.

Southern Experiment Station Directors appointed a representative to the conference beginning with the 18th conference (1965). The representatives were Dr. E. V. Smith, Director, Alabama Agricultural Experiment Station for conferences 18 (1965) to 20 (1967); Dr. John H. Owen, Director, Georgia Agricultural Experiment Station for conferences 21 (1968) to 23 (1970); Dr. Walter K. Porter, Associate Director, Mississippi Agricultural and Forestry Experiment Station for conferences 24 (1971) to 38 (1985), and Dr. Gerald J. Musick, Dean of Agriculture and Director, Arkansas Agricultural Experiment Station for conferences 39 (1986) to date.

Beginning with the 14th conference (1965), one day was devoted to the discussion of research results and experiences, one-half day for the consideration and approval of the conference report, and one-half day for presentations on items of current interest (an open session beginning with the 18th conference). The next change was made with the 24th conference (1971) when a program committee was appointed. In this conference, the oral reporting session was reduced from one to one-half day; one-half day was devoted to concurrent sessions on current topics, one-fourth day to a summary of previous day's topics, one-fourth day to consideration and adoption of the conference report, and one-half day to open session on current topics.

Beginning with the 25th conference (1972), one-half day was devoted to oral reports, one-half day to consideration and adoption of the report, one-half day to the discussion of current topics in the open session, and one-half day joint session with other research conferences. The latter continued through the 33rd conference (1980) when it was discontinued.

Beginning with the 27th conference (1974), the program committee system was reorganized. The committee consisted of two representatives from the state experiment stations, one from the state extension services, and one from the U. S. Department of Agriculture. The members serve two-year terms on a rotating basis. The conference chairman continued to serve as chairman of the program committee.

Beginning with the 30th conference (1977), the program committee was expanded to include a representative from the chemical industry and from the consultant organizations. They were to present oral reports for their groups and were to serve as their representatives in the closed session for consideration and adoption of the conference report.

In recent years the program has consisted of submitted papers and the one-half day invited paper session with one-half day devoted to the adoption of the insect loss data, changes in control recommendations and the airing of mutual problems. All sessions of the conference are now open.

The conference has done much toward keeping the various segments aware of the progress that is being made in the cotton insect research and control picture. The conference has expanded from the original concept of improvements in chemical control to encompass alternative methods of controlling insects. Insect population management continues to be practiced but with less reliance on insecticides.

As indicated in the preceding discussion, the first report was actually written and unanimously adopted by conferees during the conference. The draft was taken to Washington, D. C., submitted for cursory editing to available editors and published through agency procedures of USDA'S Agricultural Research Service. Similarly, in the next few conferences, the report was started anew. Each topic was assigned to a committee of two to five members which completely revised or updated it from the preceding report based on the added year of research and experience. Thereafter, until the 14th conference (1961), a committee of two experiment station entomologists and a representative of the National Cotton Council met with ARS and other USDA entomologists in late October or November in Beltsville to prepare a working draft of the report which was considered and adopted at the ensuing conference. Beginning with the fourth conference (1950), a copy of the report was mailed to registrants of the Annual Cotton Production Conference which later became the Annual Cotton Production-Mechanization Conference. The Insecticide Sections of the reports of the 4th (1950) through the 12th conferences (1958) were typed, mimeographed and distributed to the conferees of the Annual Cotton Production Conference.

The first report (1974) of 16 pages consisted of an introduction and sections on insecticides, insects, bug catching machines, application equipment and conferees. Subsequent reports became longer as topics were added. In the interest of space, only the most significant additions are mentioned.

Resistance of Insects to Insecticides was added to the 9th report (1955), following a disastrous boll weevil outbreak in the Lower Delta of Mississippi and both the Mississippi and Red River Deltas of Louisiana.

The procedure for revising the report was changed for the fourteenth conference (1961). A series of questionnaires applicable to various sections of the report developed by a committee that met in Beltsville, Maryland were mailed to prospective conferees in September. The information in the returned questionnaires was compiled in the USDA, ARS Beltsville office and was included in the tentative draft of the conference report mailed to the conferees before the conference. The conferees were asked to suggest changes and additions to the chairman by mail. This procedure expedited the consideration and adoption of the report and made additional time available for other conference activities.

The thirty-first report of 75 pages added a section on conference highlights which was an important improvement in it and subsequent reports.

The thirty-third report (1980) of 77 pages added a table on yield losses to the cotton crop caused by various cotton insects and spider mites. This, too, was a valuable addition to the report. Past experience showed that such losses developed by the U. S. Department of Agriculture invite considerable criticism. Estimates under the auspices of the annual conference invite less criticism even though the same scientists are involved in their development. From the beginning, the development of annual estimates on cotton yield losses has been financially supported in part by The Cotton Foundation.

While the general chairman was responsible for revising, publishing, and distributing the report, it was standard procedure to have the revised report on camera copy

delivered by the end of January to the technical editor who in turn delivered it to the Office of Communication in the Department of Agriculture for publication with expected delivery of the published report by the end of February. The report was hand carried to the technical editor and to the Office of Communication, U. S. Department of Agriculture in Washington, D. C.

It might be added here that technical editors at headquarters provided cursory editing. Before tape and mag card machines became available, the changes in the report were pieced in so that it had blank spaces which affected the continuity of the report. Also, before sophisticated duplicating equipment became available, trouble was experienced in putting together and assembling the tentative drafts of the report.

In 1976, the conference chairman moved from headquarters in Beltsville, Maryland to an assignment in Stoneville, Mississippi. Thus, the thirtieth report (1977) was edited and publication arrangements were made in the ARS Southern Region Office, New Orleans, Louisiana. With the thirty-first report (1978) the technical editors made suggestions on tightening the report and that and other editions were considerably improved in appearance as well as content.

The last formal report was issued in 1984 as the 37th Annual Conference Report on Cotton Insect Research and Control. Since that time the highlights of the annual conference, changes in insect control recommendations, and insect loss data have been published in the Cotton Insect Section of the Annual Proceedings of the Beltwide Cotton Research Conferences. The conferees planned to publish and update a report after every five annual conferences have been held.

As a result of the Annual Conferences on Cotton Insect Research and Control, there is no other agricultural area with as much compatibility among State, ARS, consultant and industry personnel in the research, extension and control efforts for insects than those that attack cotton. Conferees can be justly proud of the accomplishments of the conference in its forty plus year history. No less should be expected from conferences of the future.

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Chapter 1

MAJOR DEVELOPMENTS IN MANAGEMENT OF INSECT AND MITE PESTS IN COTTON

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INTRODUCTION

The intent of this chapter is to set the stage for this monograph by providing a summary of key events leading to the state-of-the-art of insect and mite pests in cotton. Selection of the events included herein was very difficult because of the long and rich association of arthropods and cotton culture. Because cotton may be produced in the United States only in warmer regions and requires a long growing season to reach physiological maturity, it is subject to the depredations of many herbivorous (plant feeding) arthropods. Exotic pests such as the boll weevil, *Anthonomus grandis grandis* Boheman, and the pink bollworm, *Pectinophora gossypiella* (Saunders), pose particularly difficult management problems as attempts to limit their population growth often result in the development of secondary pest problems. In most regimes, cotton is grown in a virtual monoculture involving extensive areas that generally favor pest buildup and minimize the impact of naturally occurring biological control agents. The potential for losses to arthropod pests is greater in cotton than in any other field crop and no other crop has been the target of more entomological attention. As a result, many of the outstanding entomological contributions have been made by scientists studying arthropods associated with cotton culture.

INVASION OF THE UNITED STATES BY THE BOLL WEEVIL

Prior to 1892, when the boll weevil crossed the Rio Grande River near Brownsville, Texas, insect damage to cotton was largely limited to lepidopterous pests, primarily the bollworm, *Helicoverpa zea* (Boddie) and the cotton leafworm, *Alabama argillacea* Hübner. The bollworm had been recognized as a pest of cotton since 1820 (Quaintance and Brues, 1905), but damaging populations were sporadic in occurrence and rarely developed in the southeastern states.

The entry of the boll weevil into the United States is probably the single most important entomological event to have occurred in cotton. In the United States, the boll weevil found an optimal environment consisting of small cotton fields surrounded by

ample overwintering habitats that stretched from southern Texas to Virginia. By 1922, the boll weevil had added 600,000 square miles to its range, and eleven years later had infested the entire Cotton Belt except for northwestern Texas (Pencoe and Phillips, 1987). The boll weevil is the major factor responsible for the westward shift in cotton production in this country as well as the crop diversity that developed in the Southeast early in the twentieth century. Also, the boll weevil is largely responsible for the early development of the entomological profession in the southern states.

CLASSIC EARLY STUDIES ON BOLLWORM BIOLOGY AND MANAGEMENT

The classic investigation of the bollworm by Quaintance and Brues (1905) obviously deserves attention as it is an ageless example of quality entomological science. This often cited publication may be considered as the most thorough single work on the bollworm, and it has served as the foundation for all subsequent studies on biology and management of bollworms. These researchers observed temporal (of or relating to time) and spatial (of or relating to space) distribution patterns of the bollworm in agroecosystems across the Cotton Belt and developed an understanding of how host complexes, host phenologies, farming practices, weather and biological agents affected bollworm population dynamics. They were the first to conduct detailed studies of the predaceous (arthropods that prey on others) and parasitic arthropods associated with the bollworm/tobacco budworm and to recognize the important contribution that biological control agents make toward pest population regulation. Many of the cultural management tactics they recommended, particularly early crop maturity, are as relevant today as they were at the beginning of this century.

CLASSIC EARLY STUDIES ON BOLL WEEVIL BIOLOGY AND MANAGEMENT

The significance of the boll weevil as a cotton pest was recognized very soon after it entered the United States and research was initiated toward the alleviation of the problem (Townsend, 1895). The culmination of early investigations into boll weevil biology and management was a multicomponent suppression system based on cultural tactics that farmers could employ to reduce the impact of the boll weevil on cotton production (Quaintance, 1905; Hunter, 1912; Howard, 1896; Malley, 1901; Hunter and Hinds, 1905; Pierce, 1917). By the early 1920s, these scientists had developed sufficient information to form the nucleus of a sound, multifaceted pest management program for the boll weevil based on the principles of applied ecology. The specific tactics employed to promote crop earliness, and thus escape from the highest number of boll weevils in late season, in concert with thorough post-harvest crop residue destruction still serve as key components in modern day boll weevil management systems. Later investigators (Isely and Baerg, 1924; Isely, 1934) added to the repertoire by advancing the "trap crop" concept for control of weevils during early season and by demonstrating that controlled burning and clearing of favorable overwintering habitat were effec-

tive in reducing boll weevil populations. The latter is likely the major factor leading to a decline in boll weevil population levels in the Mississippi Delta since the 1950s.

CALCIUM ARSENATE PERIOD

Among the most profound developments in the control of insect pests of cotton was the discovery that calcium arsenate dust was an effective control for the boll weevil (Coad, 1918; Coad and Cassidy, 1920). These experiments demonstrated that the application of calcium arsenate on 4- or 5-day intervals, from the point when 15-20 percent of the cotton squares were damaged until boll maturity, would protect the cotton crop from boll weevil depredation. The additional discovery that calcium arsenate could be rapidly applied by aircraft, with no loss in boll weevil control effectiveness (Coad *et al*., 1924; Hinds, 1925), set the stage for a period in the history of insect control on cotton that may best be characterized as excessive reliance upon use of insecticides. Control of boll weevils with calcium arsenate made cotton production much more profitable over most of the Cotton Belt.

As an omen of future events, the extensive use of calcium arsenate often had undesirable side-effects; destruction of natural enemies of such insect pests as the bollworm and the cotton aphid, *Aphis gossypii* Glover, led to more frequent outbreaks of these pests (Sherman, 1930; Ewing and Ivy, 1943). During the period 1920 to 1945, a high percentage of research on cotton insects was devoted to the evaluation of calcium arsenate for boll weevil control and various additives as a means of controlling infestations of the cotton aphid and the bollworm/tobacco budworm (Newsom, 1974).

COTTON INSECT SCOUTING AND THE THRESHOLD CONCEPT

Very soon after demonstration of effectiveness of calcium arsenate, Isely and Baerg (1924) reported that scouting and treating as needed provided the most economical methods of utilizing the new chemical control technology. The employment of James R. Horsfall to scout cotton in Arkansas during 1926 was the genesis of systematic cotton insect scouting. Scouting became the key step beltwide in cotton insect management (Lincoln *et al*., 1975). Most of the early thresholds were derived from a research base supplemented by intuition; nevertheless, they were founded on the concept that some level of insect damage was tolerable. Eaton's (1931) early work showing the ability of the cotton plant to compensate for shedding of floral buds early in the fruiting cycle supported the threshold concept. Successful boll weevil control through use of calcium arsenate never reached its full potential because the cooperative extension service was not prepared to carry out the needed educational program and sufficient trained scouts were unavailable during that era (Lincoln *et al*., 1975). The advent of the chlorinated hydrocarbon insecticides and devastating outbreaks of the boll weevil in 1949 and 1950 brought about the general use of "scouting" in cotton (Isely, 1950; Lincoln, 1951). Adoption of scouting and the threshold concept across the Cotton Belt

led to widespread acceptance of integrated pest management (IPM) as a general practice in the 1970s.

THE PINK BOLLWORM AS A PEST OF COTTON IN THE UNITED STATES

The pink bollworm was first found in the United States in Texas in 1917, but rigid quarantine and cultural control programs prevented the pest from causing widespread economic problems until the early 1950s (Newsom and Brazzel, 1968). Similarly, the pink bollworm was discovered in Florida in 1932, but an eradication program conducted during 1932-36 eliminated the pest from the commercial cotton producing counties of northern Florida and southern Georgia; has not been a pest in the Southeast since. Since that time, the pink bollworm has been known to exist in the eastern United States only on wild cottons in southern Florida (Noble, 1969).

In 1952, the pink bollworm caused serious losses to the cotton crop in southern Texas which resulted in a joint state and federal research effort designed to provide means for immediate control of the pest. The program was highly successful and by the late 1950s the infestation had declined and losses were minimal. The objective of the program was to reduce the overwintering population of pink bollworms to such an extent that damaging infestations did not develop during the subsequent growing season. This was accomplished by early crop maturity, use of defoliants or desiccants for rapid boll opening to facilitate machine harvesting, early harvesting, early crop residue destruction, winter and early-spring irrigations in desert areas and uniform planting of cotton during a designated period to allow moths to emerge and die before cotton fruit was available for oviposition. Proper ginning techniques and sanitation ensured that no larvae overwintered in stored or waste cottonseed (Bottrell and Adkisson, 1977). The pink bollworm provides a classic example of a major pest of cotton that may be successfully managed through a combination of cultural controls, sanitation and quarantine tactics when employed over a wide area.

The pink bollworm has become a key pest in Arizona and southern California since the mid-1960s and its management in the irrigated regions of the West has been much less successful than in Texas. The practices of long-season production and stubbing (ratooning) of cotton resulted in the development of a pink bollworm pest problem of major proportions in the irrigated West. The situaton was exacerbated by more frequent outbreaks of secondary pests in response to increased insecticide used to control pink bollworm. During the late 1980s, the problem was ameliorated through the regulatory prohibition of stubbing and the general application of more stringent pest management practices.

INTRODUCTION OF THE SYNTHETIC ORGANIC INSECTICIDES

No single event in the history of cotton production in the United States, other than perhaps the spread of the boll weevil across the Cotton Belt, impacted the cotton agroecosystem and cotton production more dramatically than the introduction and use of the synthetic organic insecticides. The general use of these insecticides shortly after World War II quickly revolutionized prevailing attitudes and practices of growers and entomologists toward cotton insect control. With the introduction of DDT followed by benzene hexachloride, toxaphene, chlordane, aldrin, heptachlor, dieldrin, endrin and others, cheap and highly effective insecticides were available for the first time to combat insect pests of cotton. Technological advancements in formulations led to the development of emulsifiable concentrates which were more convenient to use than dust formulations. They were easier to package, transport, store, handle and apply.

Initial successes with these new chemicals were so spectacular that cotton production systems were radically modified to take maximum advantage of the new technology. Cultural practices were rapidly adopted to attain the goal of maximum yields. By the early 1950s, many of the growers in the South had adopted a "womb-to-tomb" or "wash day" program of insecticide application. Treatments began with seedling emergence and terminated with crop maturity. Hence extensive treatment of the crop with insecticides provided an inexpensive, reliable and high-return form of insurance. Ecological principles of regulating pest populations that had been effective against boll weevil and other pests were quickly forgotten or completely ignored for almost two decades by most growers and entomologists (Newsom, 1974).

Subsequently, organophosphorous compounds such as parathion, methyl parathion, azinphosmethyl (Guthion®), demeton (Systox®), EPN, and the carbamates such as carbaryl (Sevin®) were developed and widely used, often in combination with organochlorines. The prevailing philosophy was toward further exploitation of the chemical control technology as new and more complex arthropod pest problems arose.

EMERGENCE OF NEW PEST PROBLEMS IN RESPONSE TO INSECTICIDE USE

Sherman (1930) was perhaps the first to observe an outbreak of a secondary pest in response to insecticide use in cotton. He reported that bollworms were much worse in fields where calcium arsenate had been used for boll weevil control, but he had no explanation for the event. Later Ewing and Ivy (1943) confirmed Sherman's observation by showing that the use of insecticides could cause an increase in bollworm infestations resulting from loss of natural enemy efficiency. The emergence of the cotton aphid as a cotton pest following use of calcium arsenate for boll weevil control (Gaines *et al.*, 1940) is another early product of the disruption of naturally-occuring biological control agents.

Observations were reported that the new organic insecticides were highly toxic to a

wide variety of arthropods other than pest species. Soon after, resurgence of pest populations and the emergence of new pests were observed. It was demonstrated as early as 1947 that the organochlorine insecticides were much more toxic than calcium arsenate to the predaceous arthropod complexes in cotton fields (Newsom and Smith, 1949). These authors observed that predator population densities were reduced more in cotton plots treated with organochlorines than in plots treated with calcium arsenate. Also, bollworm/ tobacco budworm populations were found to be inversely proportional to predator populations.

Within a few years of the introduction and widespread use of the synthetic organic insecticides on cotton, the bollworm evolved from an occasionally occurring pest to a major pest occurring annually across much of the Cotton Belt. During the same period, the tobacco budworm, *Heliothis virescens* (F.), arose from relative obscurity to become a major cotton pest. Spider mites, previously unknown as pests of cotton over most of the Cotton Belt, also achieved widespread pest status. Other arthropod pests have followed this same pattern as a consequence of synthetic organic insecticide usage.

DEVELOPMENT OF INSECT STRAINS RESISTANT TO INSECTICIDES

The use of insecticidal mixtures temporarily solved problems resulting from changes in pest status of various arthropod species. For example, BHC-DDT-sulfur mixtures gave excellent control of the insect pest complex of cotton and satisfactory suppression of spider mites for several years. The prevailing philosophy of insect control during this era was to add another insecticide to the spray tank as new pest problems developed.

A far more serious problem began to develop within five years after chlorinated hydrocarbon insecticides were adopted for general use on cotton; resistant populations of the cotton leafworm and the cotton aphid were reported (Newsom, 1970). The significance of this phenomenon was not realized until resistance to the chlorinated hydrocarbon insecticides in populations of boll weevil in Louisiana was reported in 1955 (Roussel and Clower, 1957). In the case of the boll weevil, the major change was increased use of insecticide mixtures or wholesale switches from the organochlorines to the organophosphates. To date, the boll weevil has not developed strains resistant to the organophosphates, and representatives of that chemical class are still widely used for weevil management.

Control difficulty with the bollworm/tobacco budworm complex was first encountered during the late 1950s when field efficacy of DDT decreased. Resistance to DDT in strains of bollworms/tobacco budworms generally occurred across the Cotton Belt by 1970, and populations of these species were resistant to endrin, carbaryl (Sevin®) and toxaphene-DDT by 1980 (Sparks, 1981). The switch from chlorinated hydrocarbon insecticides to organophosphates, notably methyl parathion, provided a short-term solution. Methyl parathion resistance in the tobacco budworm appeared in Texas in the late 1960s (Whitten and Bull, 1970) and in most other regions of the United States

Cotton Belt during the 1970s. Although organophosphorous insecticide resistance in the bollworm was reported for several states, the levels of resistance were much lower than those in tobacco budworm (Sparks, 1981).

Since the introduction of the pyrethroids in 1978 as highly effective, economical insecticides for bollworm/tobacco budworm control on cotton, there has been great concern that their overuse would result in the development of pyrethroid resistant strains. This concern was particularly relevant because DDT and the pyrethroids have demonstrated degrees of cross-resistance (Sparks, 1981). Since the mechanism of resistance was known to be of the knockdown resistance or target insensitivity type, bollworm or tobacco budworm strains possessing the resistance gene would be resistant to all pyrethroids (Plapp *et al*., 1989). As predicted, resistant strains of the tobacco budworm have developed in response to intensive selection pressure by pyrethroids (Crowder *et al*., 1984; Martinez-Carrillo and Reynolds, 1983; Luttrell *et al*., 1987; Staetz, 1985). A coordinated effort of pyrethroid resistance management is currently underway in the United States to stem pyrethroid resistance development in the tobacco budworm (Plapp *et al*., 1990). This program has been embraced by most cotton producers, consultants, extension workers and chemical industry representatives in hopes of continued successful use of the pyrethroids on cotton, as replacement insecticides are yet undeveloped.

The success of this resistance management strategy appears threatened by proponents of full-season cotton insect control who advocate the "womb-to-tomb" philosophy of insect control with little regard to the economic threshold concept and the application of insecticides based upon need. Entomologists have warned that the short-term benefits accrued through full-season application of insecticides do not justify creation of the catastrophic problems that are known to be products of the overuse of insecticides. But, history seems to have a way of being repeated.

Resistant strains of many other arthropod pests (e.g. cotton aphid, beet armyworm) of cotton have developed across the Cotton Belt in response to our insecticide use patterns, but these are too numerous for discussion here. A complete discussion of the insecticide resistance phenomenon is presented by the National Research Council (1986).

DEVELOPMENT OF SYNTHETIC DIETS FOR COTTON INSECTS

Among the most significant research achievements on cotton insects were the early nutritional studies which led to the development of synthetic diets for boll weevil, pink bollworm and the bollworm/tobacco budworm (Vanderzant and Reiser, 1956; Vanderzant and Davich, 1958; Vanderzant *et al*., 1962). The contributions of R. T. Gast Laboratory (Mississippi State, Mississippi) toward mechanized rearing and mass production of cotton insects must also be noted (Gast, 1961). Many others contributed toward the present technology for laboratory rearing of large numbers of quality insects which, in most aspects, physiologically and behaviorally mimic their field-produced counterparts. Rapid advancements in the knowledge of insect diapause,

pheromones, resistance, nutrition and many other critical entomological areas have been achieved since the advent of artificial diets and other rearing technology.

REPRODUCTION-DIAPAUSE CONTROL OF BOLL WEEVIL

As previously reported, entomologists early in this century recognized that the boll weevil was most vulnerable to management tactics applied during the overwintering period; thus, cultural controls were employed against the late-season population. However, the diapause phenomenon in the boll weevil was not described until 1959 (Brazzel and Newsom, 1959). Once the diapause phenomenon and its temporal (of or relating to time) development was described, the concept of "reproduction-diapause" control of the boll weevil was advanced (Brazzel *et al*., 1961; Lloyd *et al*., 1966). This system is based on denying diapausing boll weevil populations access to the amount of food required to accumulate sufficient fat to successfully overwinter. A combination of insecticide applications, chemical defoliation, rapid harvest and stalk destruction is employed to achieve the objective of killing outright or starving weevils that would otherwise constitute the overwintering population. Where the "reproduction-diapause" control system has been enacted over a wide area, boll weevil populations in the subsequent year often have not reached economically damaging levels (Rummell and Frisbie, 1978). Much of the success of the Southeast Boll Weevil Eradication Program must be attributed to the proper application of this technology as it is the "backbone" of the program (Brazzel, 1989).

THE DISCOVERY, DEVELOPMENT AND UTILIZATION OF PHEROMONES

Soon after Karlson and Luscher (1959) coined the term "pheromone" to designate chemical substances secreted by an animal to influence the behavior of other animals, laboratory and field tests confirmed pheromone communication in the boll weevil (Bradley *et al*., 1967; Cross and Mitchell, 1966; Cross *et al*., 1969; Keller *et al*., 1964). The design and construction of an olfactometer (Hardee *et al*., 1967) that permitted rapid, accurate assessment of air-borne odors was a significant development that led to the isolation, identification and synthesis of the boll weevil pheromone (Tumlinson *et al*., 1969).

Pheromones were demonstrated in the tobacco budworm and bollworm in the early 1960s (Gentry *et al*., 1964; Berger *et al*., 1965), but their identification was not accomplished until ten years later (Roelofs *et al*., 1974; Tumlinson *et al*., 1975). At about the same time, the sex pheromone of the pink bollworm was identified (Hummel *et al*., 1973; Bierl *et al*., 1974).

Over the past two decades, very significant advancements in pheromone technology have occurred. Synthetic pheromones and dispensing systems are now commercially available for the major insect pests. Pheromones are key components of management and eradication programs for they are the only practical tools available for effectively

detecting low-level pest populations. The evaluation of control strategies and studies of population dynamics and dispersal are among the research areas significantly enhanced through pheromone technology. Furthermore, the use of pheromone systems to disrupt sexual communication and to annihilate males appears to be a promising management tactic for the pink bollworm (Henneberry and Beasley, 1984). Similar concepts may eventually be employed as components in management or eradication programs for the boll weevil and the bollworm/tobacco budworm.

THE EVOLUTION OF THE INTEGRATED PEST MANAGEMENT CONCEPT

The conflict between California entomologists—one group advocating insect control with chemicals and a competing group that wanted to utilize biological controls to regulate insect pest populations—spawned the first use (Stern *et al.*, 1959) of the term "integrated pest control." The concept emphasized the integration of the tactics of biological control and chemical control toward the alleviation of insect pest problems. This approach received impetus from the phenomena of pest resistance to insecticides, pest resurgence, secondary pest outbreaks and widespread environmental ailments that had become frequent problems associated with the increased dependency on organic insecticides for insect pest control. While there was general agreement among entomologists that this single-method approach to effective insect control was neither possible nor desirable, many felt that the integrated control concept needed to be expanded to embrace all possible control tactics. A much broader concept, "pest management", rapidly evolved in which all available techniques are evaluated and may be consolidated into unified programs designed to manage pest populations so that economic damage is avoided and adverse side effects on the environment are minimized (National Academy of Sciences, 1969). The contemporary integrated pest management concept (IPM) became a political and intellectual entity during the 1970s through a major research program known as "The Huffaker Project" (Perkins, 1982). This National Science Foundation/ Environmental Protection Agency supported project assumed a lead role in providing the mechanisms for multidisciplinary plant protection as a component of crop production.

Other programs initiated in the 1970s that significantly advanced the IPM concept were: (a) pilot projects for implementing extension pest management programs in all cotton-producing states; (b) pilot pest management research projects within the USDA's Agricultural Research Service; (c) the project of the Consortium for Integrated Pest Management (CIPM); and (d) curriculum development for training and certification of crop production specialists by the land-grant universities. These actions were paralleled with an intensification of integrated pest management research within state agricultural experiment stations and federal agencies financed by both state and federal sources.

The IPM concept requires an indepth knowledge of the agroecosystem to be successfully implemented. The analysis of all factors and processes in the crop's produc-

tion and protection, and the effects of abiotic factors on these development processes as well as their interactions is far too complex for intuitive solutions. It was soon realized that a new technology was needed that could utilize the power of computers and systems analysis in a manner similar to that pioneered by the fields of engineering, industry and commerce. Computer technology has been developed and is now utilized in all phases of IPM, environmental monitoring, biological monitoring and the information delivery systems. Crop production models are being perfected that will guide farmers and consultants toward optimal decision making for increased profitability. Promising developments in the areas of expert systems and artificial intelligence provide even greater hope for the future.

The culmination of the IPM concept and its promotion has been the development of ecologically sound pest management systems that are both effective and economical. Multitactical management programs have evolved to replace the programs of the 1950s and 1960s that almost solely relied on chemicals for insect control. These more sophisticated, modern-day systems are made possible because of a much expanded knowledge of the agroecosystem, computer technology and a great increase in trained personnel from the public as well as private sectors.

According to Adkisson (1986), IPM has had two major impacts: one on science and the other on agricultural production. Scientifically, IPM research has expanded our knowledge of basic ecological and physiological principles governing insect population dynamics, insect behavior and crop-pest interactions. It has also pioneered the use of systems science in agriculture. Furthermore, IPM has reshaped crop protection philosophies and has provided the mechanism for long-term, more sustainable agricultural productivity.

There are numerous outstanding examples that could be used here to document the impact of the IPM concept on cotton production in the United States, but none more impressive than the "short-season" cotton production systems that were developed in Texas in the 1970s (Parker *et al.*, 1980; Namken *et al.*, 1983). Entomologists, agronomists, economists and other cotton specialists structured low-input production systems which minimized insect damage potential and the problems previously associated with total reliance on chemicals for insect control. The short-season concept resulted in increased profitability of cotton production in all regions of Texas where it could be practiced and impacted cotton production systems across the Cotton Belt. Other notable cotton IPM programs include the "Community-Wide Bollworm Management Program" implemented in Arkansas (Phillips *et al.*, 1980; Frisbie *et al.*, 1983) and the "Optimum Pest Management Trial" conducted in Mississippi (Hamer *et al.*, 1983). These IPM programs and the concepts upon which they are based will be discussed in more detail in other chapters of this monograph.

INTRODUCTION OF THE PYRETHROID INSECTICIDES

The pyrethroids were introduced as a new class of insecticides in the United States cotton market in 1978. They offered great promise for insect pest control because they

were highly effective, particularly against bollworm/tobacco budworm, and they did not pose the environmental problems associated with other organic insecticide classes. Problems of persistent residues and biological magnification in food chains (typical of many organochlorines) and acute toxicity and adverse effects on crop physiology (typical of certain organophosphates) were not associated with the pyrethroids. For the first time, highly effective insect control could be achieved on cotton without obvious adverse environmental effects.

The pyrethroids gave a decade of unparalleled cotton insect control and provided a "fail-safe" mechanism that allowed for the unprecedented application of the economic threshold concept. Therefore, they were far superior to other insecticide classes for IPM programs. Throughout most of the Cotton Belt, management programs based upon pyrethroid use ensured minimum losses to insect pests and maximum crop production potential. Overall cotton production, on a per-acre basis, for the first ten years following introduction of the pyrethroids, was the highest in history.

The many positive attributes of the pyrethroids have led to greater dependence on this class of chemicals, not only for control of insects on cotton, but on many other crop hosts of cotton pests. Furthermore, the simplicity of insect management afforded by the pyrethroids has led to a ground-swell of support for return to the philosopy of full-season insecticide control that prevailed during the 1950s and 1960s. This short-sighted approach threatens the long term existence of the pyrethroids as effective tools for cotton insect management. Strains of the tobacco budworm that are resistant to the pyrethroids have evolved in many United States cotton production regions in response to the intensive selection pressure of current management programs. The return to sensible approaches to insect control, including resistance management strategies for the pyrethroids, is an absolute necessity because of a rapidly declining insecticide arsenal.

BOLL WEEVIL ERADICATION

Elimination of the boll weevil from the United States Cotton Belt became the goal of entomologists and the cotton industry very soon after the pest entered Texas in the late 1800s. Early attempts at eradication failed because the necessary technology was unavailable; thus the concept of boll weevil eradication lay dormant for 50 years.

The successful eradication of the screwworm, *Cochliomyia hominovorax* (Coquerel) from the southeastern United States, and resistance to the chlorinated hydrocarbons in Mid-South boll weevil strains provided impetus for revival of the goal of boll weevil eradication. The introduction and passage of a resolution at the 1958 annual meeting of the National Cotton Council, which declared the boll weevil as the number one enemy of cotton production, signaled a renewed effort to eradicate the boll weevil from the United States (Perkins, 1982). This resolution resulted in monies to construct the Boll Weevil Research Laboratory (Mississippi State, Mississippi). This Laboratory developed and refined the technologies, which justified pilot eradication tests leading to operational eradication programs.

THE PILOT BOLL WEEVIL ERADICATION EXPERIMENT (PBWEE)

The three-year Pilot Boll Weevil Eradication Experiment (PBWEE) (1971-1973) was designed to determine the technical and operational feasibility for eliminating a boll weevil population from a delineated area by use of available population suppression techniques (Parencia, 1978). The PBWEE was jointly conducted by federal and state personnel in southern Mississippi. Results of the PBWEE were inconclusive as boll weevils were found in pheromone traps within the core area during program evaluation and there was no way to acertain their origin (Perkins, 1982; Pencoe and Phillips, 1987). The general conclusion was that the basic technology necessary to achieve eradication required improvements in several areas and that further demonstrations must be conducted in a region with greater isolation.

THE BOLL WEEVIL ERADICATION TRIAL (BWET)

The Boll Weevil Eradication Trial (BWET) was conducted in northeastern North Carolina and adjacent Virginia from 1978 to 1980 to demonstrate conclusively that eradication of the boll weevil was technically possible. The site chosen provided the desired degree of isolation from other cotton producing regions. The BWET was a much more successful program as results indicated that it was highly probable (0.9983 level of probability) that the native boll weevil population was eradicated from the core evaluation area (Knipling, 1983; McKibben and Cross, 1984). Though cotton in North and South Carolina is now weevil free, it is continually monitored in such a way to maintain this status. The expanded program in Georgia, South Alabama, and Florida is in the final stages of eliminating the boll weevil as an economic pest. Suppression comparable to that obtained in the original North Carolina/South Carolina program appears attainable.

BELTWIDE ERADICATION PROGRAM

The successful results from the Boll Weevil Eradication Trial (BWET) provided the incentive to extend the eradication program from North Carolina westward across the Southeast. The program has passed through the Carolinas and is in the latter stages of completion in Georgia, Florida and South Alabama. The boll weevil is no longer an economic pest in the Carolinas, Georgia, Florida and Southeast Alabama. While total elimination (eradication) of the species appears improbable, the BWET results and subsequent benefits to the cotton industry in the area confirm that total population management over a large geographic region may be the optimum management strategy to employ against the boll weevil in the Southeast (Carlson and Suguiyma, 1983).

A boll weevil eradication program was initiated in the western United States concurrently with the expansion of the southeastern program (Brazzel, 1989). Boll weevil populations have been dramatically reduced in the West (Arizona and California), and it is no longer viewed as an economic pest.

A thorough discussion of the above eradication programs including the specific technology utilized in each is presented in Chapter 19 of this book.

SUMMARY

Because of the limitations imposed on cotton production by arthropods, entomologists over the past century have diligently sought methods to limit growth of arthropod populations or to eradicate them. Many technological advancements have been made toward understanding insect behavior and physiology and the interactions of insects with their hosts and other arthropods. Much progress has been achieved toward describing insect population dynamics and the many factors affecting insect numbers. Management tactics and systems have been developed and effectively utilized as well as exploited. The challenge of beltwide boll weevil eradication remains. However, continued success of southeastern and southwestern eradication programs justifies the belief that the boll weevil eventually can be eliminated as an economic pest in the United States.

Cotton insect management will remain an exciting and dynamic endeavor characterized by the resolution of one problem and the genesis of another, ad infinitum. Presently, the silverleaf whitefly, *Bemisia argentifolii* Bellows and Perring, and its biotypes pose a perplexing problem of mammoth proportions, particularly in the desert valleys of the Southwest. What will be the next challenge for cotton entomologists?

SECTION I

CHARACTERIZATION OF INSECTS AND MITES

Chapter 2

BIOLOGY AND ECOLOGY OF IMPORTANT INSECT AND MITE PESTS OF COTTON

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INTRODUCTION

More than 100 species of insects and spider mites are pests of cotton in the United States. Fortunately less than two dozen species are common on a yearly basis and will cause major crop losses to extensive acreage if not controlled. The remaining species can cause severe economic loss, but usually only in limited geographic areas during occasional years or when a particular beneficial arthropod complex has been disrupted.

This chapter provides a brief description of the developmental stages of major pests, enabling their identification, and provides general information on development of the life stages of particular species or for species groups. Damage symptoms, geographic distribution, hosts, pest phenology and ecological conditions that favor or limit pest outbreaks also are discussed. For a complete list of the pest species attacking cotton in the United States see Anonymous (1984a). More detailed information on the major and minor pests not mentioned is usually available through the cooperative extension services and the state universities in the cotton producing states.

SQUARE AND BOLL FEEDING INSECTS

BOLL WEEVIL

Boll weevil, *Anthonomus grandis grandis* Boheman

Identification and Development of the Stages—Three forms of *Anthonomus grandis grandis*—the Mexican boll weevil, the thurberia weevil and the southeastern boll weevil—occur in the United States with only the southeastern boll weevil being found in all cotton growing areas except the California San Joaquin Valley. Anatomically, they are very similar and can intermate, but genetic differences exist between these strains (Bartlett *et al.*, 1983) and their identity can be differentiated. The adult boll weevil (Plate 2-1[1]) is a snout weevil that is somewhat variable in size and color, ranging from 1/8 to 1/3 inch (3.2-8 mm) long, and from reddish brown to dark gray. Overall weevil size is due largely to the nutritional condition of the host squares or bolls. Color changes from reddish to dark brown or gray with aging. Weevils with black integument may occur, but this color strain is not common under field conditions (Bartlett, 1967; McGovern *et al.*, 1974).

The immature stages of the boll weevil are always found within cotton squares and bolls which they hollow out as they feed. Eggs, which may be found by dissecting squares in which boll weevils have recently oviposited (laid eggs), are slightly elliptical in shape, opaque and about 1/25th inch (1 mm) long. Shortly before hatching, the brown head capsule of the larva may be seen through the egg wall. Total developmental time of the boll weevil from egg to adult ranges from 11 to 67 days, depending on temperature. At a typical summertime temperature of 86F (30C), development takes between 14 and 22 days (Hunter and Pierce, 1912; Isely, 1932; Fye *et al.*, 1969; Bacheler *et al.*, 1975; Cole and Adkisson, 1981). The larvae are white, legless grubs, while the pupae are similar to the adult since the external features of snout, legs and wings are visible through the pupal cuticula (Hunter and Hinds, 1905; Parrott *et al.*, 1970; Roach, 1973).

Host Plants—In the United States, the southeastern boll weevil is primarily restricted to cotton for feeding and oviposition (egg laying), while the thurberia weevil is primarily restricted to a wild cotton, *Gossypium thurberi* Tod., in parts of Arizona (Cross *et al.*, 1975; Burke *et al.*, 1986). Also, in Arizona the boll weevil may feed and survive on globe mallow, *Sphaeralcea* spp., but cannot reproduce (Palumbo, 1985). The boll weevil originated in Meso-America (i.e. Central America and Southern Mexico) therefore, many native host plants have been reported from Central and South America but most do not occur in the United States (Burke *et al.*, 1986). The number of seasonal generations ranges from two to eight, depending on length of the growing season (Fenton and Dunnam, 1929; Hopkins *et al.*, 1969; Sterling and Adkisson, 1971); however, the generations overlap and the average is closer to three per year in most areas.

Damage Symptoms—When boll weevils enter cotton, either from overwintering sites or through migration, the number necessary to cause economic damage depends on factors such as physiological condition of the cotton plant, phenological stage of plant development and weather patterns. Fecundity (egg laying ability) is higher in first brood females than in later females primarily due to plant maturity and the

[1]All color plates can be found in the Appendix of this chapter.

decreasing number of squares available for oviposition by the later broods (Fenton and Dunnam, 1929; Fye and Bonham, 1970). Rates of population increase per generation have been estimated by several researchers, and range from 1- to 9.6-fold, depending on environmental conditions (Knipling, 1960; Walker and Hanna, 1963; Lloyd *et al.*, 1964). Numbers of adults necessary to cause economic losses are quite low. Lloyd and Merkl (1966) found that overwintered weevil populations of 14, 25, 50 and 100 weevils per acre damaged 0, 28, 46, 66 and 83 percent of the available squares, respectively, while second-generation weevils damaged from 84 to 96 percent of the squares. In another study, Roach *et al.* (1971) indicated that more than 50 percent of all squares were punctured when the F_1 population exceeded 1000 per acre and 80 percent were punctured when the population exceeded 2000 per acre. Boll weevils both feed on and oviposit in cotton fruit, therefore their damage is easily discerned. Both sexes chew small holes into the fruit and yellowish frass (solid insect excrement) is usually present around the feeding area. The female oviposits (lays eggs) within the holes, then seals them with frass solidified with fluid from her excretory tract (Plate 2-2) (Cushman, 1911). Most squares with oviposition punctures will flare open and abscise from the plant within eight days, whereas older bolls may remain on the plant and result in damaged locks where the eggs were oviposited and the larvae developed.

Phenology[2] and Population Dynamics—Boll weevils overwinter as diapausing adults in woods litter and similar cover adjacent to the previous season's cotton fields (Brazzel and Newsom, 1959; Hinds and Yothers, 1909; Hunter and Hinds, 1905). Diapause in boll weevils is an induced dormancy. Diapause is the result of a complex interaction of photoperiod, temperature, physiological condition of the cotton plant, low night temperatures in the adult stage and boll feeding in the larval stage (Lloyd *et al.*, 1967; Earle and Newsom, 1964; Carter and Phillips, 1973; Cobb and Bass, 1968). Mortality of diapausing boll weevils during the winter is generally high, particularly in the more northern cotton growing regions, and is primarily dependent on the condition of weevils and the severity of winter weather conditions (Bondy and Rainwater, 1942; Fenton and Dunnam, 1929; Rummel and Carroll, 1983; Sterling, 1971; Taft *et al.*, 1973).

Spring emergence of boll weevils from overwintering quarters appears to be dependent on an accumulation of hours above a temperature threshold of 52F (10.85C), and possibly the time they entered overwintering quarters in the fall (Jones and Sterling, 1979; Rummel and Carroll, 1983; Mitchell *et al.*, 1973). In most areas of the Cotton Belt, spring emergence occurs from April through June, although diapausing weevils have been found in woods trash in all months of the year except July and August (Beckham, 1963).

The life span of emerging overwintered weevils is dependent on the availability of cotton for food in the spring. Fenton and Dunnam (1929) indicated the average longevity of weevils emerging prior to cotton emergence was 5.65 days (range 1 to

[2]Phenology is a branch of science that deals with the relationship of climate and periodic biological phenomena or behavior of insects.

52), and 8.13 days (range 1 to 40) on cotton prior to fruiting. On fruiting cotton, longevity was 19.39 (range 2 to 69) for males and 16.05 days (range 2 to 48) for females. This contrasts with the 70- to 80-day average indicated by Hunter and Hinds (1905), but agrees with data given by Fye *et al.* (1959). Mating occurs prior to entering diapause and females deposit fertile eggs in the spring without remating (Fenton and Dunnam, 1929; Walker and Pickens, 1962). However, overall reproductive potential of females increases significantly with spring remating (Taft *et al.*, 1963; Roach, 1979). The oviposition behavior of the boll weevil has been investigated by several workers and, in general, the females prefer half-grown cotton squares, but will lay multiple eggs in most sizes of squares and bolls when field populations are high (Hunter and Hinds, 1905; Cushman, 1911; Jenkins *et al.*, 1975; Lloyd *et al.*, 1961).

Mortality of developing immature weevils in squares can be quite high due to predation, parasitism and high temperatures, but more than 50 percent will usually emerge as adults (Fenton and Dunnam, 1929; Smith, 1936; Bacheler *et al.*, 1975; Chesnut and Cross, 1971). These newly emerged weevils will mate and begin ovipositing after five to eight days, unless they are subjected to cool temperatures or diapause-inducing conditions (Fenton and Dunnam, 1929; Roach, 1979; Cole and Adkisson, 1981).

Interfield movement and long range migration can occur in any summer brood of weevils (Isely, 1926; Roach *et al.*, 1971; Roach and Ray, 1972). Most mass movements of weevils apparently occur when fields become heavily infested and few oviposition sites remain (Fenton and Dunnam, 1929; Fye and Bonham, 1970). The direction of movement seems to be random and possibly wind-aided. Migrating individuals are known to move up to 45 miles (Davich *et al.*, 1970; Beckham and Morgan, 1960).

After feeding on cotton, male boll weevils produce a chemical pheromone that attracts both male and female weevils to the food source (Bradley *et al.*, 1968; Hardee *et al.*, 1969). Thus, it serves as both an aggregation and sex pheromone in this species, and is extremely important in the ability of migrating weevils to find and infest cotton fields.

BOLLWORMS AND TOBACCO BUDWORMS

Bollworm, *Helicoverpa zea* (Boddie)
Tobacco budworm, *Heliothis virescens* (Fabricius)

Identification and Development of the Stages—Eggs are laid singly, generally on new terminal growth. Newly-laid eggs are pearly-white, becoming darker with age. Prior to hatching, a brownish ring characterizes the upper portion of the egg (Plate 2-3). There are consistent differences between the eggs of the two species that can be seen with a stereoscopic microscope (Neunzig, 1964; Werner *et al.*, 1979). Tobacco budworm eggs have fewer ridges from bottom to top and the ridges terminate before they reach the tiny micropyle (minute opening in insect egg through which sperm enter) at the middle of the top. At least part of the ridges reach the micropyle on eggs of the bollworm. There are usually 10-12 of these ridges on tobacco budworm eggs and 12-15 on eggs of the bollworm.

Young caterpillars (larvae) are yellowish or reddish, with large black bumps (tubercles) on the body (Plate 2-4). Mature stages reach a length of 1-1 1/2 inch (26-38 mm) and vary in color from pale green to dark brown, often with a pattern of paler markings on the back and sometimes with a pronounced dark band on the sides. The dark bumps of the first instar are less conspicuous on later stages and the integument of the body contains many tiny spines, which are visible with a hand lens, especially on dark parts of the skin.

Third-instar or later caterpillars of the two species can be distinguished from each other with a hand lens. At this stage they are 3/8 inch (9 mm) long or greater. Tobacco budworm caterpillars have tiny spines, like those on the skin, extending onto the slightly enlarged dorsal bumps on the first, second, and eighth segments behind the true legs. Bollworm caterpillars lack spines on these bumps. Another positive character is the presence of a tooth-like structure on the inner face of the mandible of the tobacco budworm that is absent from the bollworm.

Adult moths, which may be found resting on leaves in the field, are very different in the two species. Tobacco budworm moths have three oblique dark bands on the front wings and are usually olive-green (Plate 2-5). Bollworm moths (Plate 2-6) are almost uniformly pale buff, with some small dark flecks on the front wings with a slightly paler crescent in the middle of the wing (Werner *et al.*, 1979)

Damage Symptoms—Damage to cotton by larvae of the bollworm and tobacco budworm cannot be distinguished. Upon hatching, the young larvae tunnel through young terminal leaf buds and tiny squares. The young squares turn brown and may be mistaken for plant bug injury. Larvae then move to larger squares, cutting a hole in the side of the square and feeding on the floral structures. Such squares will turn yellow, flare and drop from the plant (Brazzel *et al.*, 1953).

Larger larvae demonstrate a preference for squares, but will feed on bolls of all sizes, making an irregular-shaped entrance hole. In many instances the entire contents of the boll are consumed. Usually, a semi-solid, moist frass accumulates outside the entrance hole. Where fruit is in short supply with high population densities, larvae can be found feeding on older cotton leaves.

Distribution—The tobacco budworm is found throughout most of the Western Hemisphere. The species is apparently most abundant in the tropics and extends through the West Indies and South America as far south as Argentina (Neunzig, 1969). Neunzig (1969) reports that the range of the corn earworm (same as bollworm) is sympatric (occupying same geographic range) with that of the tobacco budworm.

The bollworms can cause damage to cotton in any area of the Cotton Belt. However, the tobacco budworm is not a pest of cotton in the San Joaquin Valley and only as late as 1972 became a serious pest of cotton in the lower desert areas of the Southwest (Watson, 1974).

Alternate Hosts and Outbreak Contributions—Bollworms/tobacco budworms are general feeders, having a wide variety of cultivated and wild host plants (Snow and

Brazzel, 1965). Tietz (1972) listed 31 host plants for the tobacco budworm and 106 hosts for the bollworm. Corn appears to be the preferred host of the bollworm and tobacco and cotton are major hosts of tobacco budworm (Lincoln, 1972).

The host ranges for both species dictate the relative importance of host-plant complexes in the widely-separated geographic regions and diverse agroecosystems. Barber (1937) and Neunzig (1963) cite hosts of bollworm/tobacco budworm in the Southeast, while Roach (1975) stated that bollworm/tobacco budworm populations in South Carolina, especially those in early spring and fall, depend on only a few major plant species. Harding (1976) indicates that in the Lower Rio Grande Valley both species build up to damaging numbers on cultivated hosts and use wild hosts to maintain the species when cultivated plants are not available.

Seasonal activity of bollworm/tobacco budworms extends over a longer period than does the growing season of any single species of host plant. A survey conducted by Rathman and Watson (1985) indicated that abundance of bollworm/tobacco budworms on desert annuals in the Southwest is difficult to measure since hosts are widely scattered and attractive to ovipositing moths for relatively short periods of time. Populations on wild hosts also appear to be extremely variable from year to year. Ornamentals and cultivated crops are more predictable food sources than desert annuals, whose abundance is dependent upon adequate winter rainfall. Nevertheless, several wild desert plants appear to be important early-season hosts and obviously help bridge the gap until cotton and other summer hosts are available.

Phenology and Population Dynamics—Many researchers have conducted life history studies on both the bollworm and tobacco budworm. In general, developmental time is quite similar. During summer conditions, the egg hatches in three to four days. Both species pass through five or six larval instars in as little as 12 days, and drop to the soil where the pupal stage lasts 9 to 10 days in a cell one to two inches (2.5-5 cm) below the soil surface. A complete life cycle may take as little as 25 days in midsummer and there may be six to eight generations in a season (Werner *et al.*, 1979).

Tollefson and Watson (1981) determined developmental times and damage to cotton during June, July and August near Phoenix, Arizona. In June, larvae that feed primarily on squares have significantly longer developmental times than July and August larvae that feed mostly on bolls. The average duration of prepupal and pupal stages in the soil is similar for all infestation periods. Constant temperature studies showed that greatest fecundity occurred at 77F (25C) and that longevity of both sexes declined as temperatures were increased. A moth usually expends most of its reproductive capacity within the first 7-10 days of its life.

Survival in much of the Cotton Belt is dependent upon individuals entering diapause in the fall. In Arizona, Potter and Watson (1980) found the tobacco budworm to exhibit a weak diapause that occurred during the last two weeks of October. Development can be continuous in Arizona, southern California, and some southern areas of cotton production in Texas, Louisiana (Brazzel *et al.*, 1953; Graham *et al.*, 1972) and Florida. Early-season legumes, e.g., crimson clover in the South (Roach, 1975) and alfalfa in

the West (Rathman and Watson, 1985), are believed to be important hosts which support the first generation each year.

The ecological conditions favoring population increase of these pests are complex, therefore it is difficult to predict the exact circumstances that create an outbreak. Number of host plants and host sequence, as well as temperature and humidity, are important in permitting the full biotic potential of any bollworm/tobacco budworm population. However, these insects are vulnerable to effective biological control by parasites and predators and many bollworm and tobacco budworm outbreaks are insecticide-induced. Therefore, careful management of the total pest complex in cotton is of utmost importance to prevent destruction of the natural enemies at a critical time in the bollworm/tobacco budworm:cotton developmental cycles.

PINK BOLLWORM

Pink bollworm, *Pectinophora gossypiella* (Saunders)

Identification and Development of the Stages—The pink bollworm (PBW) is a small mottled, grayish-brown moth (Plate 2-7) belonging to the family Gelechiidae. It is slender and about 3/8 inch (9.5 mm) in length. The forewings are dark brown with irregular black areas; the hind wings are silvery-gray. The oval, white eggs, laid in "clusters," are about 1/25 inch (0.5 mm) by 1/50 inch (0.3 mm) in size. The first three larval instars are creamy white with dark brown heads and thoracic shields. At times the third larval instar will show transverse pinkish lines, changing into dark-pink bands in the fourth instar (Plate 2-8). Pupae are about 2/5 inch (8 mm) in length by 3/32 inch (2.5 mm) wide and exhibit a typical mahogany brown color (Werner *et al.*, 1979).

Damage Symptoms—Prior to the availability of bolls, pink bollworm infestations can be detected by the presence of "rosetted blooms," blossoms on which the petals are webbed together. Later, the first-instar larva may indicate its presence in bolls by conspicuous mines along the inner carpel wall, a result of not burrowing directly into the inner part of the boll. Other visible signs of damage include the small, round holes through which the larvae exit the bolls, and discolored lint and seed, where larvae have fed. Rotted bolls may also indicate the presence of the pink bollworms. The exit hole allows the entrance of boll rotting fungi (Watson, 1977).

Geographical Distribution—The pink bollworm was first reported from India in 1842. From there it has spread to all major cotton-producing countries of the world. Pink bollworm was first found in the United States near Hearne, Texas, in 1917. From there it spread both eastward and westward. Eastward spread of the pink bollworm apparently is limited by greater rainfall. It first was found in eastern Arizona in 1926. An eradication effort in the Salt River Valley of Arizona in the late 1950s virtually eliminated the pink bollworm from central Arizona where it had become established. However, in the early 1960s it again became established in Central Arizona, a "coincidence" with the growing of stub cotton and increased cotton production in Mexico to the South. By late 1965, it had completed its spread across Arizona and into the

Imperial Valley of California (Noble, 1969). The pink bollworm is not widely established east of Texas and Oklahoma or in the San Joaquin Valley of California. Adults are apparently carried into the San Joaquin Valley by winds from southern California. Small numbers of larvae are occasionally found in that Valley (Anonymous, 1984b).

Alternate Hosts and Outbreak Contributions—Although plants of worldwide distribution representing 7 families, 24 genera and 70 species have been recorded as alternate hosts, cotton is the preferred host of the pink bollworm. Most of the hosts belong to the Malvaceae family, of which, the genus *Hibiscus* ranks high in the insect's preference. The six cultivated plants which serve as alternate hosts are okra, *Hibiscus esculentus* L.; kenaf, *Hibiscus cannabinus* L.; roselle, *Hibiscus sabdariffa* L.; muskmallow, *Hibiscus abelmoschus* L.; castorbean, *Ricinus communis* L.; and jute, *Corchorus olitorius* L. (Noble 1969). None of these is considered to be important to the population dynamics of this pest in the arid Southwest. The severity of infestations is almost entirely associated with the way the cotton production system is managed. A long-growing season and short host-free period is conducive to pink bollworm outbreaks (Watson *et al.*, 1978).

Phenology and Population Dynamics—A generalized life cycle of the pink bollworm for a temperature of 86F (30C) is as follows: egg, 4-5 days; larval stage, 15-20 days; pupal stage, 7-9 days; and, the preoviposition period, 2 days. The total life cycle is 28-36 days. In arid, semi-tropical areas such as Arizona where the cotton-growing season may last 9-10 months, there may be six to eight generations per year (Slosser and Watson, 1972a). In more temperate regions having shorter growing seasons, four to six generations are more likely.

Short-cycle generations will continue until daylength falls to 13 hours, after which increasingly higher proportions of the population enter diapause. The long-cycle or diapausing larvae overwinter in cotton seed, lint, surface trash or in free cocoons in the soil (Watson *et al.*, 1976).

Temperature, moisture and photoperiod are important factors affecting the pink bollworm. Termination of diapause primarily is a function of temperature and moisture. Temperatures in excess of 59F (15C) are necessary for initiating pupation of overwintering larvae. Contact moisture or high relative humidity enhances survival and pupation, especially at higher temperatures. A temperature of about 72F (22C) and contact moisture appear to be most optimum for survival and the highest rate of pupation (Watson *et al.*, 1973). During the growing season moth activity is adversely affected by unusually high temperatures, and longevity and oviposition are reduced when temperatures exceed 95F to 104F (35 to 40C). Winter mortality of diapausing larvae generally is high and areas with cold, wet conditions are most detrimental to diapausing larvae (Slosser and Watson, 1972b).

Several species of parasitic and predaceous insects and predaceous mites have been reported to attack the pink bollworm. Spiders have also been observed feeding on adults. None of these, however, have been shown to effectively reduce field populations.

PLANT BUGS

Western lygus bug, *Lygus hesperus* Knight
Tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois)
Clouded plant bug, *Neurocolpus nubilis* (Say)
Cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter)

In addition to these four species, the pale legume bug, *Lygus elisus* (Van Duzee), *Lygus desertinus* Knight, ragweed plant bug, *Chlamydatus associatus* (Uhler), rapid plant bug, *Adelphocoris rapidus* (Say) and several other Miridae are reported as occasional pests.

Species Attacking Cotton and Distribution—The tarnished plant bug is common throughout the eastern and southwestern cotton growing areas. *Lygus desertinus* (no common name) is a pest of cotton in Arizona. A western lygus bug, *Lygus hesperus*, is the most common species throughout California and Arizona. The pale legume bug also invades cotton fields in the San Joaquin Valley; however, infestations do not normally persist. The cotton fleahopper occurs throughout much of the cotton producing areas of the United States. Each species appears to occupy a particular climate and host range. There is little evidence that expansion of their geographic ranges may occur.

Identification and Development of the Stages—Adult lygus bugs are 5/32 to 3/16 inch (4.5 to 5.5 mm) long, pale green, straw yellow or reddish brown in color and with a conspicuous triangle in the center of the back (Plate 2-9). This triangle is yellow or pale green on the western lygus bugs and yellow-brown on the tarnished plant bug. Lygus species have long slender and usually reddish-brown antennae. The first and second instar nymphs are pale green and may be mistaken for aphids, but differ in moving about more rapidly and having reddish tips on their antennae. Older nymphs have five characteristic black spots on their backs (Plate 2-10)—two spots on the first segment of the thorax just behind the head, two more on the next segment, and one spot in the center of the abdomen. Older nymphs of the western lygus bug and the tarnished plant bug may be pale to medium brown in color (Anonymous, 1984b; Kelton, 1975).

Cotton fleahoppers (Plate 2-11) are uniformly pale green in color with tiny black specks all over the body (Anonymous, 1984b). They are about one half the size of lygus bugs. They do not have the reddish antennae typical of lygus bugs and the nymphs do not have the pattern of dots found on lygus bugs. Other species of fleahoppers sometimes found in cotton fields have black markings on their bodies and are similar to the cotton fleahopper in size and shape.

The clouded plant bug appears somewhat larger than lygus bugs, at 9/32 inch (6.5-7 mm) long and 3/32 inch (2.5-2.6 mm) wide. Adults are yellowish tan to brown and the legs are tan with brownish markings. The body, legs and antennae have many black and pale hairs.

All species of mirids insert their eggs into the plant tissue. The elliptical egg cap is usually flush with the plant surface and is visible under magnification. Eggs may be deposited in leaf petioles, stems or fruiting structures of the plants.

Egg development of plant bugs requires about 5 to 7 days during the hot summer period but longer during cooler weather. Development of the immature stages is most rapid in hot weather, requiring as little as 9 days for cotton fleahoppers and ll days for other species. Average total developmental time is about ll to 14 days in summer and 21 or more days during cooler periods. Adult bugs have a preoviposition period of 4 to 7 days before egg deposition begins. Numbers of eggs produced are highly variable and influenced by hosts. Individual plant bugs may produce between 30 and 70 eggs (Little and Martin, 1942; Leigh, 1963).

Damage Symptoms—Plant bugs feed on developing squares, growing points and young bolls, particularly in the terminal portions of the plants (Strong, 1968; Wilson *et al*., 1984; Leigh *et al*., 1988). Smaller developing squares fed upon by plant bugs will abscise and dry (Plate 2-12), and are commonly seen in sampling for pests with the sweepnet or drop cloth. Bracts of larger squares may flare and will be shed from the plant. Squares that remain on the plant may have darkened anther filaments where the anther sacs have been destroyed. The petals and stigmatic areas of the blooms may be distorted. Bolls on which plant bugs have fed develop darkened areas where bugs have defecated. Internally, the boll wall will develop callous tissue to which the lint may cling when the bolls open. Developing seeds on which plant bugs have fed will be shriveled, lint will not develop normally and may rot in damaged locks.

Where plant damage by *Lygus* spp. and other plant bugs is limited to square loss, plants may grow tall and whip like with few or no bolls (commonly referred to in the past as "crazy" cotton). This condition is most common where some of the earliest squares are lost, stimulating the plant to greater vegetative growth followed by continued loss of squares to further lygus bug feeding. In response to destruction of growing points, squares and fruit, cotton plants will develop many new growing points at mainstem and branch nodes, take on a many branched appearance and produce additional squares. Mainstem apex destruction usually results in a candelabra appearing plant. Nodes of plants infested with plant bugs become swollen or enlarged and internodes may be shortened. Where plant bugs have been controlled, bolls may be set at later developed fruiting positions higher on the plant, providing a dispersed appearing boll set with many blank fruiting positions (Haney *et al*., 1977).

Alternate Hosts and Outbreak Contributions—Most plant bug species that attack cotton have a wide range of native and crop hosts in a number of plant genera. The lygus bugs are major pests of alfalfa, carrot, beet, bean, crucifers and other crops, particularly when grown for seed. They may be found on many plant species in native situations (Young, 1986; Fleisher *et al*., 1987; Fye, 1980; Womack and Schuster, 1987) and on weeds in cultivated crops. A host list for the western lygus bug, *Lygus hesperus* has been developed by Scott (1977) while Anderson and Schuster (1983) and Fleischer and Gaylor (1987) provide host lists of the tarnished plant bug in the Southwest and Southeast cotton production regions. Fleischer and Gaylor (1987) provide indications of seasonal abundance of the tarnished plant bug on the native plant hosts (Figure 1) in relation to outbreaks on cotton. Host plants appear to be particularly

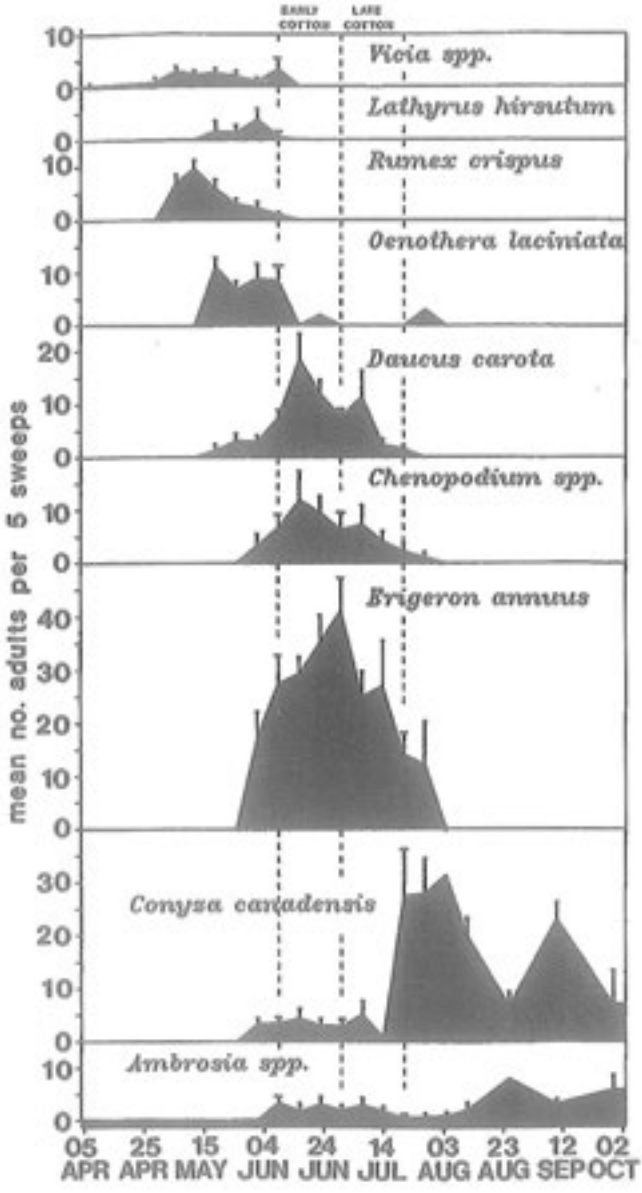

Figure 1. Seasonal abundance of adult tarnished plant bugs, *Lygus lineolaris* (Palisot de Beauvois) on hosts in the Coastal Plain Region of Alabama, providing an indication of host contribution to outbreaks of this pest on nearby cotton. (Source: Fleischer and Gaylor, 1987.)

attractive when in the flowering stage and plants in the Compositae may be preferred. *Erigeron annuus* Pers. (annual fleabane) is a common host of tarnished plant bugs, from which they may move to cotton. In the West, alfalfa (Stern *et al.*, 1967), safflower (Mueller and Stern, 1974) and weeds (redroot pigweed, *Amaranthus retroflexus* L., lambsquarter, *Chenopodium album* L. and several species of cruciferae) (Fye, 1980) in uncultivated areas and within several other crops (Leigh, unpublished data) are the principal sources of the western lygus bug. The cotton fleahopper has more than 40 reported crop, weed and native hosts, however, *Croton capitatus* Michx. (woolly croton) is the most important host of this pest (Reinhard, 1928). The clouded plant bug has more than 50 crop and wild plant hosts. Crop hosts include cotton, soybean and alfalfa. The most important wild native hosts appear to be button bush and black willow (Lipsey, 1970).

Plant bugs may migrate to cotton from their crop, native, and weed hosts at any time; however, major migrations usually occur when the spring and summer hosts mature, are harvested (Stern *et al.*, 1964, 1967), or are destroyed (Fleischer and Gaylor, 1987). For example, massive numbers of *Lygus hesperus* may appear in adjacent cotton when nearby alfalfa is harvested, as illustrated in Figure 2. Stern *et al.*

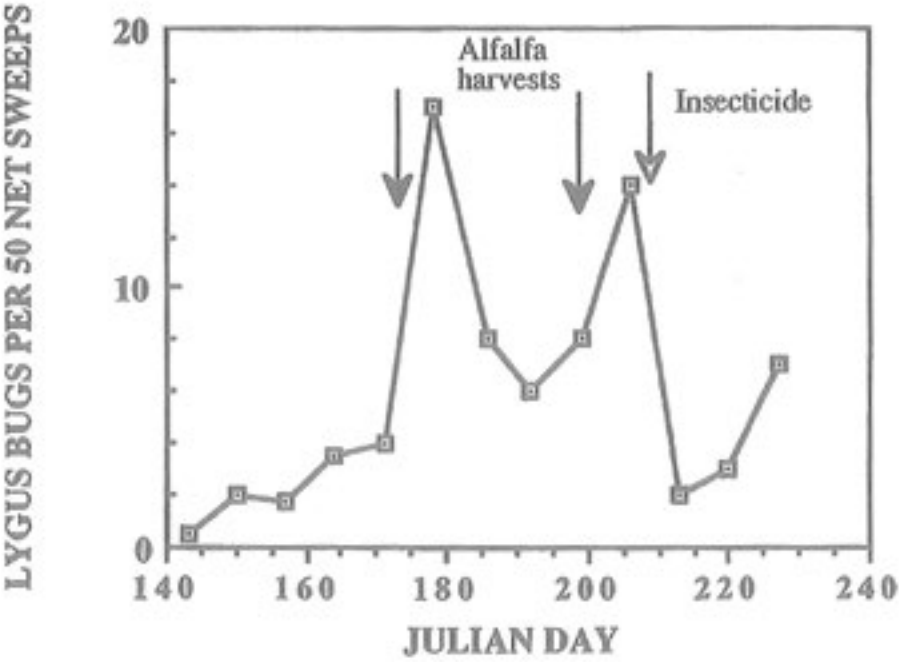

Figure 2. Western lygus bug, *Lygus hesperus* Knight, infestation level in cotton adjacent to an alfalfa field, indicating the contribution of the alfalfa crop (in relation to cutting) to infestations in cotton. (Developed from data of Stern *et al.*, 1964.)

(1967) recommend management strategies for harvest of alfalfa to attract lygus bugs from cotton and to reduce the threat of their movement from alfalfa to cotton. Fleischer and Gaylor (1987) provide suggestions for management of native and weed hosts to reduce the threat of these pests to nearby crops.

Phenology and Population Dynamics—The western lygus bugs overwinter as adults in a sexual diapause or arrested reproductive stage in suitable crop host areas (Leigh, 1966). Diapause is induced by reduced day length but is also ended in California when days become less than nine hours long (Beards and Strong, 1966). Adults become reproductive in December and on warm days will deposit eggs in available hosts from January through March. An average of 200 eggs may be deposited by an individual female over a 30-day period (Leigh, 1963). Five to seven continuous generations will develop on perennial crops such as alfalfa. One or two generations will develop on winter and spring annual hosts before movement to cotton. Three generations commonly occur on cotton. Except where large numbers of this pest migrate from crop or natural hosts, there is usually a gradual increase in bug numbers on cotton as the season progresses, without discrete generations being observed.

Tarnished plant bug phenology is very similar to that of the western species, with overwintering adults moving from groundcover to blooming plants in the spring (Crosby and Leonard, 1914). Initial infestations commonly relate to maturation of nearby weed hosts or their destruction by cultivation. In the southeastern United States, there may be at least three generations of tarnished plant bug on cotton.

The cotton fleahopper overwinters as diapausing eggs on *Croton* spp. plants (woolly croton, Texas croton, tropic croton, etc.), and hatching occurs in March and April (Sterling and Hartstack, 1979). There may be five to nine generations per year (Hartstack and Sterling, 1986) with successive generations developing on available hosts (Almand *et al.*, 1976).

As indicated in the preceding section, the magnitude of plant bug outbreaks is usually related to abundance of crop, native and weed hosts in the proximity of cotton fields. Mild winter weather, timely rainfall and cropping conditions that favor development of these alternate hosts may result in the development of high population numbers that migrate to cotton. Conditions that interfere with effective weed control in crops and timely rainfall may also result in populations of plant bugs that will move to cotton as the crops and weeds mature or are harvested. In contrast, severe winter weather, drouth and conditions that limit host growth and abundance will reduce the probability of outbreaks (Anonymous, 1984b; Fleischer and Gaylor, 1987; Fleischer *et al.*, 1988).

The magnitude of outbreaks on native or cultivated crop hosts is limited by a complex of predators and parasites provided they are not destroyed by insecticides. The most significant natural enemies are bigeyed, *Geocoris* spp., and damsel, *Nabis* spp., bugs. Wasp parasites of lygus bugs may also be locally abundant during some years (Clancy, 1968; Anonymous, 1984b; Graham *et al.*, 1986; Loan and Shaw, 1987; Dean *et al.*, 1987).

Plant bugs may occur in high numbers during the early fruiting stage of crop development. This is particularly likely in areas where there is an abundance of suitable hosts in favorable growing condition (i.e. in bloom). Frequent rainfall during winter, spring and early summer can favor buildup of most plant bug species. Later, as these hosts mature or dry as during a period of drought, plant bugs move to cotton fields (especially if irrigated) which may be the most attractive plants in an area.

Cotton plants are most vulnerable to plant bug attack in the pre-square and early-square formation period when the growing points and all small squares may be destroyed (Ewing, 1929; Wene and Sheets, 1964b; Haney *et al.*, 1977). As plants develop an abundance of squares they will tolerate low amounts of plant bug damage (Leigh *et al.*, 1988) although fruitset may be delayed somewhat. Severe infestations at any time during the fruiting period may remove all squares.

STINKBUGS

Green stink bug, *Acrosternum hilare* (Say)
Conchuela, *Chlorochroa ligata* Say
Say stink bug, *Chlorochroa sayi* Stål
Southern green stink bug, *Nezara viridula* (L.)
Brown stink bug, *Euschistus servus* (Say)
Euschistus conspersus (Uhler)
Onespotted stink bug, *Euschistus variolarius* (Palisot de Beauvois)
Dusky stink bug, *Euschistus tristigmus* (Say)
Euschistus impictiventris Stål
Redshouldered stink bug, *Thyanta accerra* McAtee

Numerous species of stink bugs, family Pentatomidae, have been found on cotton in the United States but many are predacious and only a few cause damage.

Identification and Development of the Stages—Adult stink bugs are usually oval or elliptical and somewhat flattened in shape (Plate 2–13). The antennae are five-segmented. The head appears tapered and it is much narrower than the maximum width of the pronotum (first body segment behind the head). The body length of species in this family ranges from 5/32 to 13/16 inch (4 to 20 mm), but most species present in field crops range from 1/4 to 1/2 inch (6 to 12 mm). Colors are usually shades of brown or green but some species such as the harlequin bug, *Murgantia histrionica* (Hahn), and several predacious species are brightly marked with red, orange, blue or black. Eggs of stink bugs are roughly barrel shaped (Plate 2–14) and are deposited in tight clusters, usually in multiples of seven. The eggs are usually white, light gray, green or cream, turning darker as the nymphs mature inside the egg chorion (shell). After hatching the first instar nymphs are gregarious, remain near the oviposition site and do not feed. There are five nymphal instars and the average length of time per instar is 4.5, 6.0, 8.0, 8.0 and 12.0 days for the first through fifth instars, respectively. Nymphs resemble adults with developing wing pads becoming visible in the fourth instar and

approximate adult size being reached in the fifth instar (Esselbaugh, 1946; Decoursey and Esselbaugh, 1962; Slater and Baranowski, 1978; McPherson, 1982; Brewer and Jones, 1985).

Southern green and green stink bugs are bright green insects ranging in length from 1/2 to 5/8 inch (14 to 17 mm) and 1/2 to 3/4 inch (13 to 19 mm), respectively. However, the green stink bug can be easily identified by the presence of a forward projecting spine on the second abdominal sternite (between the last pair of legs) and the long, tapering scent-gland channels. The southern green stink bug has no spine and the scent-gland channels are tear shaped. *Chlorochroa* spp. are bright green, elongate-oval species with numerous white spots scattered over the dorsal surface. They are larger species (over 7/16 inch (11 mm) in length) and are mostly found in the western and southwestern states. The various species of *Euschistus* are brown dorsally, greenish-yellow ventrally, and are similar in shape and size at 3/8 to 9/16 inch (10-15 mm) in length. Species separation is often difficult without detailed descriptions or use of dimorphic keys. Species in the genus *Thyanta* are generally pale green and are smaller than *Nezara, Acrosternum*, and *Chlorochroa* (less than 4/16 inch (11 mm) in length). They also lack a spine on the second abdominal segment. Due to seasonal color variation (individuals may be brown or white spotted due to photoperiodic influences) and close similarity among species, confusion exists in the old literature concerning which species of *Thyanta* was observed or identified as occurring in a particular area. Several species of *Podisus*, which are predacious on other insects, also can be found in cotton and may be confused with the brown stink bugs, *Euschistus* spp. Coloration of *Podisus* spp. is very similar to *Euschistus* spp. but generally *Podisus* spp. are slightly smaller, have sharper lateral pronotal angles (upper surface of first segment behind the head), and have a thick rostrum or feeding tube that is not held against the underside of the head in a groove (Morrill, 1910; McPherson, 1982; Cassidy and Barber, 1939; Furth, 1974).

Damage Symptoms—Stink bugs feed by inserting their slender mouthparts into plant tissues or seeds and extracting enzymatically liquified material. Initial signs of feeding damage are often invisible to the naked eye but later, black spotting may appear on the surface of the plant. Secondary bacterial infection may cause browning. In cotton bolls, cell proliferation resulting in callous growth or a warty appearance on the inside of the carpel wall may be present. Blackened and shriveled seed also may occur and, when bolls open, one or more locks may be hardlocked or destroyed. Extensive feeding by adult and immature stink bugs on small cotton bolls causes shedding. However, older bolls are less often attacked and damage may be insignificant or limited to one or two locks (Morrill, 1910; Wene and Sheets, 1964a; Little and Martin, 1942; Jones, 1918).

Alternate Hosts—Most species of stink bugs affecting cotton have a wide range of hosts and cotton is attacked primarily when preferred hosts are senescent or unavailable. In early season, green stink bugs feed on developing terminals and fruits of a wide range of plants including black cherry, elderberry, dogwood, wheat, cowpea and

coffee senna, *Cassia occidentalis* L. They usually produce one generation prior to entering fruiting cotton. Brown stink bugs feed on crucifers, alfalfa, clover, various weeds (such as white top fleabane and common mullein), peas, sorghum and berry plants as well as most vegetables. They may be present in cotton throughout most of the season, but do little damage until the cotton is fruiting (Schoene and Underhill, 1933; Jones and Sullivan, 1982; Morrill, 1910; Jones, 1918; Underhill, 1934; Rolston and Kendrick, 1961; Woodside, 1947).

Phenology and Population Dynamics—All species of stink bugs affecting cotton can produce one or two generations per season on cotton, depending upon latitude, available feeding site and temperature. In the more southern areas of the United States, as along the Gulf Coast and southern Texas, four generations may occur on a succession of host plants. In more northern areas one to one and one half generations may occur. Diapausing adults overwinter; few if any nymphs survive the winter. Spring emergence from overwintering sites occurs March through May, depending on latitude. Some adults may be active periodically during the winter in southern Texas and other subtropical areas but reproductive activity begins with increasing spring temperatures. Generation development takes from 38 to 60 days, depending on species and temperature. Normally, only the second generation is a problem on cotton throughout most of the Cotton Belt. In the West, the consperse and western brown stink bugs may move to cotton in massive numbers from maturing seed alfalfa and grain sorghum, respectively. Since cotton fruit set from June through August constitutes most of the lint that will be harvested, this is the period when cotton is most vulnerable to stink bug damage. The proximity to good overwintering sites and an abundance of wild host plants for the emerging overwintered adults contribute significantly to the chances for stink bug problems in cotton (Little and Martin, 1942; Jones and Sullivan, 1982; Morrill, 1910; Jones, 1918; Woodside, 1946).

ARMYWORMS

Beet armyworm, *Spodoptera exigua* (Hübner)
Fall armyworm, *Spodoptera frugiperda* (J. E. Smith)

The beet armyworm is an occasional pest of cotton and may become severe under certain environmental conditions, particularly in the San Joaquin Valley of California and the gulf coast states (Alabama, Louisiana, Mississippi and Texas) (Essig, 1926). The fall armyworm occurs in the tropical and subtropical Americas and is an occasional pest of cotton in the southeastern United States (Sparks, 1979). Fall armyworm is most common where grasses and corn are grown (Folsom, 1932).

Identification and Development of the Stages—The moth of the beet armyworm is mottled gray with light markings and a wing expanse of 1 to 1 1/2 inches (2.54–3.81 cm) (Todd and Poole, 1980). They deposit masses of eggs on the upper surface of leaves (Plate 2-15) that are beneath the uppermost canopy of leaves. These egg masses, which are revealed by pushing aside the upper leaves, are covered with the gray-white

body scales of the moths. The tiny, newly hatched larvae have black head capsules and they feed gregariously (Plate 2-16). Later instars are usually pale olive green in color with a dark stripe down the back and pale stripes on the sides (Plate 2-17) and usually have a black spot on the sides of the second body segment (over the second thoracic leg). They may grow to 1 to 1 1/2 inches (2.54 - 3.81 cm) in length when fully developed. There is considerable color variation with some maturing larvae being nearly black-green while others may be pale green.

The fall armyworm adult is similar in appearance to the beet armyworm (Todd and Poole, 1980), but slightly larger 1 1/4 to 1 inches (3.18–3.81 cm) in length. It produces egg masses similar in appearance and location on plants to the beet armyworm. The large larvae have a prominent white inverted "Y" on the head capsule, three fine yellowish stripes down the back, with a dark band on either side, below which there is an ill-defined lighter colored band. They also have prominent tubercles (pimple-like structures) on the back in a pattern similar to that of the bollworm (Little and Martin, 1942).

Damage Symptoms—Early instar larvae of both species skeletonize leaves adjacent to and on which egg masses are laid. Fourth and fifth instar larvae may feed in and destroy the terminals of small cotton plants. Older larvae of infestations that develop in July will feed on bracts, large squares and young bolls and, in heavy infestations, can remove all fruiting forms in that stage of development. Square loss in early season can be replaced by new squares, but a major reduction in yield may occur since squares produced from late July on may not produce bolls that can mature before harvest (Eveleens *et al.*, 1973).

Feeding by early-stage fall armyworm larvae usually is restricted to grasses in weedy fields. Migration to cotton usually is by the larger larvae which can cut off branches and defoliate plants.

Alternate Hosts—The beet armyworm attacks a number of plants in several plant families. Lambsquarter, *Chenopodium* spp., appears to be a preferred late spring and summer weed host in California, and larvae can be collected from alfalfa and sugarbeet throughout the year.

The fall armyworm has a wide range of hosts including Coastal bermudagrass, corn, other grains and grasses, but they will feed on peanut and cotton in the absence of these preferred hosts (Sparks, 1979; Pitre *et al.*, 1983).

Phenology and Population Dynamics—The beet armyworm overwinters in most southern Cotton Belt states and the San Joaquin Valley in the larval stage on actively growing hosts such as alfalfa and sugarbeet, but larval growth is decreased by cool temperatures. Moth flights occur in May, mid- to late-June, mid- to late-July, and late-August through September.

The fall armyworm overwinters only in Florida, southern Texas and the tropical Americas (Sparks, 1979). Successive broods of moths migrate northward and can invade the entire Cotton Belt east of the Rocky Mountains. This habit of migration

enables them to escape high levels of parasitism and predation during severe outbreak years (Little and Martin, 1942; Pair *et al.*, 1986).

Outbreaks of the beet armyworm may occur in the spring of the year and appear to relate to an abundance of suitable hosts and a prey:predator imbalance. Seedling stage outbreaks on cotton can occur when infested weed hosts are present in the cotton field and weed removal by cultivation leaves only cotton on which to feed. Outbreaks on fruiting stage cotton occur when beet armyworms build to high numbers on nearby alfalfa, sugarbeet or other crop hosts and the moths move to cotton to oviposit. These crops usually have insecticides applied that destroy natural enemies, particularly predators such as the minute pirate bug, bigeyed bugs and damsel bugs (Eveleens *et al.*, 1973) and the parasite *Hyposoter exiguae* (Vier.) (van den Bosch and Hagen, 1966). July and later outbreaks on cotton are common during years of drought and also can be traced to application of insecticides that have destroyed the natural enemies of this pest.

Climatic conditions that provide an abundance of host grasses appear to favor the fall armyworm. Outbreaks also appear to be favored by their ability to migrate ahead of their natural enemies. Outbreaks of fall armyworm that affect cotton are more likely to occur during late summer. However they can occur at any time of the year particularly when cotton fields contain grassy weeds.

LEAF FEEDING INSECTS AND MITES

SPIDER MITES

Carmine spider mite, *Tetranychus cinnabarinus* (Boisduval)
Desert spider mite, *Tetranychus desertorum* Banks
Fourspotted spider mite, *Tetranychus canadensis* McGregor
Pacific spider mite, *Tetranychus pacificus* McGregor
Schoene spider mite, *Tetranychus schoenei* McGregor
Strawberry spider mite, *Tetranychus turkestani* Ugarov and Nikolski
Tumid spider mite, *Tetranychus tumidus* Banks
Twospotted spider mite, *Tetranychus urticae* Koch
Tetranychus ludeni Zaker
Tetranychus yustis McGregor

Ten species of spider mites are reported to attack cotton in the United States (Anonymous, 1984b). At least 23 additional species attack cotton worldwide (Leigh, 1985).

The twospotted spider mite is recorded from cotton throughout the United States and much of the temperate and subtropical world and the strawberry spider mite from that region of the northern hemisphere. Similarly, the carmine spider mite occurs in most tropical and subtropical cotton producing areas. Other spider mite species are more restricted in distribution, perhaps as a result of host and climatic factors. While there may be potential for more widespread distribution of some spider mite species

through future commerce, the majority of them may already occupy situations to which they are best adapted.

Identification and Development of the Stages—The spider mites that attack cotton are microscopic in size and ovate in shape (Plate 2-18). They may be observed with a 10X magnifying glass or hand lens. The mature females are less than 3/64 inch (0.13 mm) long. Adult male spider mites are smaller than the females, and have a tapered abdomen. Mature adult females usually are pale greenish with some variation in color and in distribution of the dark spots within their abdomen. Diapausing or recently molted spider mites may lack these dark spots and be ivory or pale orange to red in color.

The carmine and twospotted spider mites, which are most commonly cited as pests of cotton in the United States, are identical in their morphology. However, the carmine spider mite is light carmine in color and has been separated from the twospotted spider mite by differences in host plant preference, biology and color, as well as through cross mating studies (Jepson *et al.*, 1975). The body of adult females of the desert spider mite is reddish in color. Adult females of the twospotted, strawberry and other spider mite species usually tend to be greenish in color with dark interior abdominal spots that have typical distribution in some species; however, distribution of the spots is variable and not a reliable identification factor.

Immature stages of the several spider mite species appear similar to the adults, although the young carmine and desert spider mites lack the distinctive coloring of the adults. Newly hatched mite larvae possess only six legs while later stages have eight legs.

Spider mite eggs are found on leaf surfaces or on webbing within colonies. They are spherical and translucent when first laid and become opaque, ivory or faintly brownish before hatching.

Detailed identification of the several spider mite species is provided by Baker and Pritchard (1953) and by Jeppson *et al.* (1975). Positive identification usually requires males of the species mounted on a microscope slide and under high magnification. They are identified by the shape of the male aedeagus or copulatory organ. Field identification of some species, based on plant injury, is possible by workers who are very experienced.

Spider mites develop through an egg and three immature stages before becoming adults (Jepson *et al.*, 1975). At higher favorable temperatures, the egg stage may require as little as two days, and each immature stage a little more than one to two days. Between each stage there is a quiescent or immobile phase of a few hours. A complete generation may require only 8 to 12 days. At cooler temperatures this may be extended to nearly one month (Figure 3).

Damage Symptoms—Spider mites can colonize all foliar and fruiting portions of the cotton plant. They most commonly are located in colonies on the under surface of cotyledons and leaves. There may be significant species differences in appearance of these colonies, ranging from compact colonies near the base of the leaf or in leaf folds

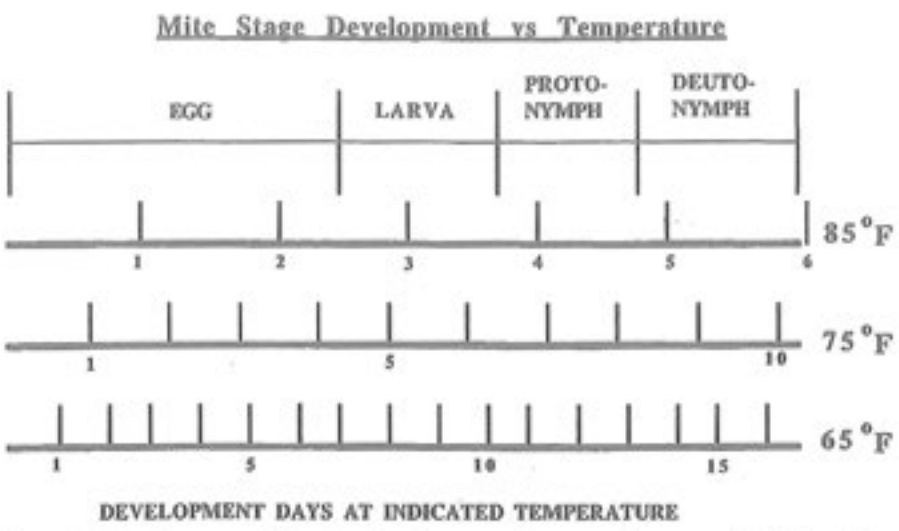

Figure 3. Developmental time in days for growth stages of twospotted spider mites, *Tetranychus urticae* Koch, in response to three temperature regimens. (Developed from Carey and Bradley, 1962.)

to wide dispersion over both leaf surfaces (Jepson *et al.*, 1975; Leigh and Burton, 1976). The strawberry spider mite appears to be unique in causing abscision of infested leaves (Leigh and Burton, 1976), square and boll shed and death of severely infested plants. There are reports of similar defoliation by the carmine and twospotted spider mites in some regions of the world. Areas may develop in cotton fields where there are few or no leaves present and very few bolls. The other spider mite species cause various degrees of leaf-scarring and leaves exposed to the sun may turn red (Smith, 1942). As a result there will be large areas of reddened leaves (Plate 2-19). Apparently, damaged tissue is not as photosynthetically active as undamaged leaves, and there is general debilitation of infested plants, shedding of squares and small bolls and incomplete fiber and seed development.

Alternate Hosts—The several spider mite species that attack cotton have a wide range of hosts in numerous plant families, with some species recorded as having between 100 and 150 hosts. Leigh (1985) provides a generalized host and distribution summary for the species that attack cotton throughout the world. There are major differences in host preference among spider mite species. In addition to cotton, common crop hosts are alfalfa, bean, carrot, corn, cucurbitaceous plants, eggplant, peanut, safflower, soybean, many compositae and landscape plants. In the natural environment, there are many broadleafed weed plant hosts including nightshades, mallows, morningglories, daisies, etc. (Jepson *et al.*, 1975).

Phenology and Population Dynamics—In warmer climates several spider mite species continue to reproduce throughout the winter if there are suitable hosts, but

most species will enter diapause if there is an absence of growing plants. In colder climates adult mites seek shelter and enter diapause, usually in cracks of bark on perennial hosts, in the crowns of other plants (Jepson *et al.*, 1975) and in the soil near the base of hosts. Diapausing forms may appear in most populations under adverse conditions such as declining host quality. High numbers of spider mites may develop on spring and early summer hosts and result in continuous reproduction through spring and summer with no distinct generations.

Spider mite numbers may be greatly reduced by winter conditions. They increase rapidly on spring and early summer hosts, particularly where they are able to escape their natural enemies or in crops where natural enemies have been suppressed by pesticide applications. Spider mites may appear in cotton fields when plants first emerge from the ground or at any time during the growing season. Infestations may develop slowly during cool spring weather and then seemingly explode with onset of hot summer weather. Infestation buildup is strongly enhanced by hot dry weather and conditions that suppress the presence and numbers of several predators (Figure 4).

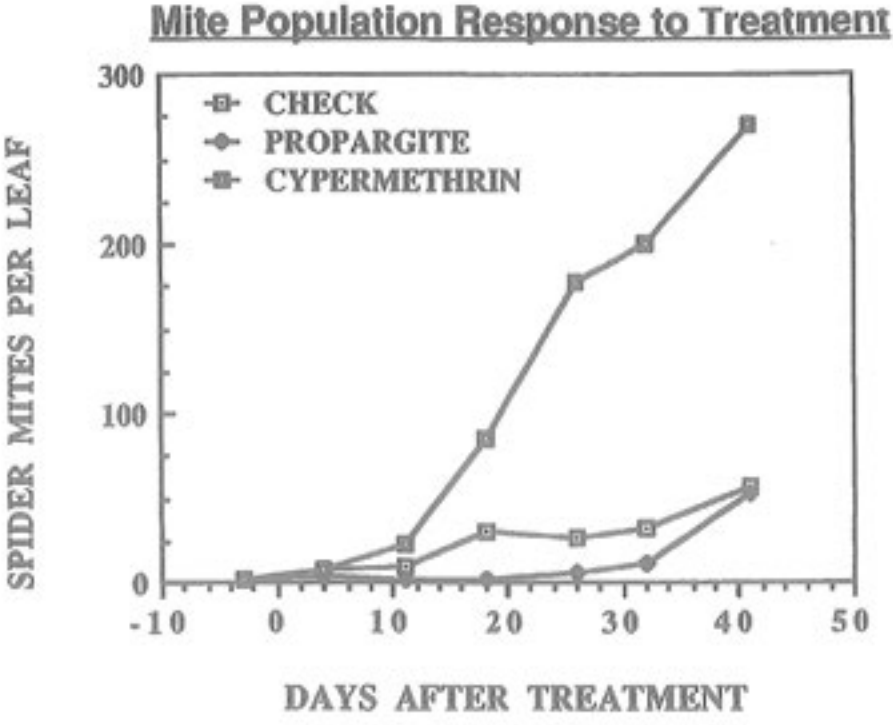

Figure 4. Pacific mite, *Tetranychus pacificus* McGregor: population response to natural conditions (absence of insecticide use), treatment with a selective acaricide or treatment with a broad spectrum insecticide, California San Joaquin Valley.

In undisturbed situations, i.e. where broad spectrum insecticides are not used, gradual maturation of the plants during August and buildup of predator numbers will cause a general decline in spider mite numbers.

Spider mites are generally favored by hot dry conditions (Cannerday and Arant, 1964). A number of species demonstrate their greatest potential for increase at temperatures near 86-90F (30-32C). The carmine and desert spider mites can not survive temperatures at or near 50F (10C). Longevity and reproduction in most species declines greatly above 100F (38C). Moderate humidities appear to be most favorable to most spider mite species although there are wide differences in humidity tolerance (Andres, 1957; Nickel, 1960). Extreme low humidities may result in reduced reproduction (Jepson *et al*., 1975)

High relative humidity interferes with molting of the developing stages and several species will enter a quiescent stage at extremely high humidity. In areas where humidity is commonly high, viral and fungal diseases may decimate spider mite infestations (Muma, 1955; Carner and Cannerday, 1968, 1970; Jepson *et al*., 1975). The favorability of molting conditions and absence of conditions favoring disease organisms may account for the perennial severity of spider mites in arid climates.Spider mites may be abundant in the soil in arid climates and on alternate hosts when cotton seedlings emerge from the ground. Frequent spring winds may blow spider mites into cotton fields at any time. Early infestations on cotyledons and first leaves may be evident but can be masked by the flush of vegetative growth that occurs with the onset of hot weather. Mites will move into the upper foliage under increasing population pressure and as vegetative growth is slowed by nutrient requirements of developing bolls (Leigh, 1984).

FOLIAGE FEEDING CATERPILLARS

Alfalfa looper, *Autographa californica* (Speyer),
Cabbage looper, *Trichoplusia ni* (Hübner)
Cotton leafworm, *Alabama argillacea* (Hübner)

Species Attacking Cotton and Distribution—The larvae of more than a dozen species of moths feed on leaves of cotton plants and may cause severe defoliation. The beet armyworm, southern armyworm and cotton leafperforator are discussed elsewhere in this chapter. The alfalfa looper is not a significant pest and is mentioned only because the moths and larvae are very similar in appearance to the cabbage looper and are often confused with it.

The cabbage looper is native to North America and occurs throughout the United States and in Canada and Mexico. The alfalfa looper occurs throughout the western United States, but is reported on cotton only in California. The cotton leafworm is native to the tropical Americas and frequently invades gulf coast cotton fields. Occasionally the cotton leafworm will invade cotton in the low desert regions of California and Arizona.

Identification and Development Stages—Moths of the cabbage looper are grayish-brown in color, about an inch long with a wingspread of nearly 1½ inches (38 mm). The mottled brownish front wing has a distinctive small silvery spot near the middle resembling the "figure 8" or a "question mark". The alfalfa looper is slightly larger than the cabbage looper. They are very similar in color and appearance but the silvery spot of the alfalfa looper is more in the shape of a "gamma" (Y) mark. The cotton leafworm moths (Plate 2-20) are olive-tan color with three wavy transverse bars on the forewings; they are 1 1/4 inches (32 mm) from wingtip to wingtip.

The larvae of these three "worm" pests can be distinguished from other "worms" by their looping action as they crawl (Anonymous, 1984b). Larvae of both the alfalfa and cabbage loopers are very similar in appearance—long, slender, and green with faint whitish longitudinal lines, with true legs on the first three segments and prolegs on the fifth and sixth abdominal segments (Plate 2-21). The cabbage looper has nipple like vestigial prolegs on the third and fourth abdominal segments; they are lacking on the alfalfa looper (Okumura, 1961). The cotton leafworm, which is a semilooper (Plate 2-22), is very distinctive from the other two loopers in being yellowish green to dark green in color with three narrow white stripes down the back and a white line along each side (Little and Martin, 1942). Distinctive spots on the dorsum are paired white rings surrounding a dark spine on each segment. Fully grown larvae of each species are about 1 1/2 inches (38 mm) long.

The pale yellowish, ribbed eggs of the alfalfa and cabbage (Plate 2-23) loopers are hemispherical, while the eggs of the cotton leafworm are ribbed and somewhat flattened. The eggs of all three species usually are laid singly on the lower surface of fully developed leaves.

Damage symptoms—Newly hatched larvae feed on the lower leaf surface, producing semi-transparent windows. Larger worms consume the interveinal tissue, leaving only the veinal skeletons of leaves. Older leaves are usually consumed first, but the plants may be completely defoliated.

Alternate Hosts—Larvae of alfalfa and cabbage loopers are very general feeders with a wide range of crop and weed hosts (Essig, 1926). The cabbage looper generally demonstrates preference for cruciferous plants. The cotton leafworm is capable of reproducing only on cotton, although larvae may occasionally feed on other hosts (Little and Martin, 1942). Adults of the three species will feed on nectar of many plants.

Phenology and Population Dynamics—The alfalfa looper overwinters in the pupal and adult stages (Essig, 1926). There are two generations per year, occurring in late May to early June and in July. This insect usually is controlled on its many hosts by parasites and predators although considerable leaf-ragging may occur on cotton during the early squaring stage. Economic infestations of alfalfa looper have not been encountered although it is sometimes the target of pesticide use.

The cabbage looper is not known to overwinter in the California San Joaquin Valley where it occurs annually as a pest. It may reinvade that valley each season. It usually

is under excellent control by naturally occurring parasites and predators. There are usually three generations per year occurring in July through September. Potentially severe infestations are often controlled by a naturally occurring polyhedrosis virus. This disease is common in late-season populations. Outbreaks of cabbage looper are most likely to occur where vegetable hosts are grown and where the biological control agents on cotton or other hosts have been destroyed through use of insecticides.The cotton leafworm is a tropical insect that does not overwinter in the United States and must reinvade this country each year. During outbreak years it usually first appears along the gulf coast in Texas, Louisiana and Alabama. Cotton leafworm outbreaks usually occur following a rain in years of above average summer rainfall. This suggests that the moths are carried into the United States on tropical storm fronts. There can be three generations in the United States. There are many natural enemies of the cotton leafworm in its native habitat, and both generalist parasites or predators and some specialist natural enemies may increase in numbers to decimate the third generation. Birds can be effective predators of this pest.

COTTON LEAFPERFORATOR

Cotton leafperforator, *Bucculatrix thurberiella* Busck

The cotton leafperforator occurs in the southern United States, in Tropical Central America and in Australia (Schmutterer, 1977). In the United States it is a pest only in Arizona and southern California (Anonymous, 1984b).

Identification and Development of the Stages—The cotton leafperforator is a small, elongate, whitish moth (Plate 2-24). The wings are narrow, lanceolate, and the margins are fringed with very long hairs. The antennae are long and the head is concealed by a tuft of short white hairs on the upper surface. Wing span is only about 1/4 to 1/3 inch (6.3-8.4 mm) (Metcalf *et al.*, 1962). Female moths lay minute, bullet-shaped eggs, upright, usually on the lower leaf surface. The caterpillar cuts directly through the egg base and into the inner part of the leaf where it starts its mine (Werner *et al.*, 1979). Development continues as a leaf miner (Plate 2-25) for the first three instars at which time the fourth instar moves to the leaf surface. The fourth and fifth instars (Plate 2-26) are surface feeders, interrupted only by a resting stage (referred to as the horseshoe stage) between instars. During this resting period, it is protected by a loosely-spun web surrounding the U- or horseshoe-shaped larva. After completing the fifth instar it spins a slender, ribbed, whitish cocoon in which it pupates on the leaves, stems or sometimes on the soil (Watson and Johnson, 1972).

Damage Symptoms—At first, damage appears only as small mines in the leaves, increasing in size with each subsequent instar. After the fourth instar emerges to the surface of the leaf, the larva eats only to the opposite epidermis. Feeding occurs on both upper and lower surfaces. During daylight hours the larvae generally feed on the lower surface of the leaf. When disturbed, both fourth and fifth instars wriggle vigorously, usually dropping from the leaf on a silken thread and returning when the dis-

turbance is over (Watson and Johnson, 1972). Severely damaged leaves take on a scorched appearance due to the windows of necrotic tissue.

Alternate Hosts and Outbreak Contributions—This insect is native on wild cotton, *Gossyspium thurberi* Tod., but thrives on planted cotton, usually first attacking field edges. Overwintering and subsequent build-up is favored in areas where cotton is grown as a perennial (stubbed or ratoon) plant. Populations are generally low and held in check by a complex of tiny parasites and predators. Outbreaks usually follow applications of insecticides for control of other pest species (Werner *et al.*, 1979).

Phenology and Population Dynamics—The adult overwinters on abandoned cotton. A long, host-free overwintering period is very detrimental to survival. Seasonal development begins as soon as cotton is available. A detailed study on the biology of this pest indicates that a complete life cycle may take as little as 16 days under summer conditions to as much as 40 days under conditions similar to those in early or late season (Watson and Johnson, 1972). For example, in a constant 68F (19.8C) environment, the egg hatches in slightly over three days, followed by a three-day mining period. The exposed fourth and fifth instars require only approximately one and 2.5 days, respectively. Following a pupal period of 4.5 days and a pre-oviposition period of almost two days, the cycle begins anew (Watson and Johnson, 1972). Thus, many generations are possible each season, depending upon the length of the growing season and management practices.

The cotton leafperforator is a secondary pest; outbreaks are usually human-induced. Because it overwinters on wild or abandoned cotton, survival is directly related to the abundance of overwintering sites and the length of the host-free period. Therefore, a shorter growing season is detrimental to this pest. Additionally, any practice which reduces the use of insecticides lessens the chance of a perforator outbreak since it is usually held under excellent biological control unless its natural enemies are destroyed. This pest is resistant to most of the currently registered insecticides and has the capacity to quickly develop resistance to others, therefore; it is extremely important to manage cotton leafperforator through biological and cultural control measures.

LEAFHOPPERS

Potato leafhopper, *Empoasca fabae* (Harris)
Southern garden leafhopper, *Empoasca solana* DeLong

Species Attacking Cotton—Both the potato leafhopper and southern garden leafhopper occur throughout the Cotton Belt. They are pests of cotton primarily in the West. The southern garden leafhopper is most common in the desert valleys. It migrates to cotton when fields of its main host, sugarbeet, are dried down for harvest. Potato leafhopper damage to cotton occurs in areas of Texas and on the east side of the San Joaquin Valley. In California it migrates to cotton, citrus and other crops from California buckeye (*Aesculus californica* (Spach), its winter and spring host (Smith, 1942; Anonymous, 1984b).

Identification and Development of the Stages - The adults are about 1/8 inch (3 mm) long, by 1/4 as broad, of a general greenish color and somewhat wedge-shaped (Plate 2-27). They are broadest at the head end, which is rounded in outline, and tapered evenly to the tips of the wings. There are several faint white spots on the head and thorax. One of the characteristic marks of the potato leafhopper is a row of six white spots along the anterior margin of the prothorax. The hind legs are long, enabling the insect to jump considerable distances (Metcalf *et al*., 1962).

Beginning from 3 to 10 days after mating, the small, whitish, elongate eggs, about 1/24 inch long, are inserted into the main veins or petioles on the underside of the leaves. An average of two to three eggs are laid daily, and the females live for about a month. The eggs hatch in about 10 days and nymphal development is completed in about 14 days. The nymphs resemble the adults but lack wings and are pale green (Metcalf *et al*., 1962).

Damage Symptoms—Adults and nymphs of both species feed by sucking sap from veins on the underside of mature leaves, mostly in the lower half of the plant. Affected leaves may become distorted and leathery and may develop yellow or red blotches (Plate 2-28), a condition know as hopperburn. The most reliable symptom of leafhopper injury is that the veins are swollen and lumpy (Anonymous, 1984b). Other leafhoppers on cotton feed between leaf veins. They may cause a light-colored stippling of leaves, but they do not cause swollen veins and their injury does not result in yield loss.

Alternate Hosts and Outbreak Contributions —Adults overwinter on native plants and in plant debris. Each spring they migrate into various cultivated crops, including cotton (Werner *et al*., 1979). As mentioned earlier, in the West sugarbeet is the main host of the southern garden leafhopper, and California buckeye, *Aesculus californica* (Spach), provides the spring source of the potato leafhopper that moves into cotton, citrus and other crops (Anonymous, 1984b).

In the eastern half of the United States, the potato leafhopper is the most injurious pest of potatoes (Metcalf *et al*., 1962). It also feeds on other plants such as eggplant, rhubarb, dahlias and horsebean, producing hopperburn as well. On bean and apple, stunting, dwarfing, crinkling and tight curling of leaves are characteristic symptoms. Alfalfa leaves become yellowed and clover leaves reddened when attacked. The southern garden leafhopper is common on potato, cotton, lettuce and beans. Both species have a wide host range, feeding on more than 100 cultivated and wild plants (Metcalf *et al*., 1962).

Phenology and Population Dynamics—These two leafhoppers occur throughout the year in the southernmost parts of the Cotton Belt. With their extensive host range, they may move from one crop that is drying to another more succulent host and continue reproducing in the seasonal sequence. Natural enemies usually keep leafhoppers from building up large populations on cotton. However, when large numbers migrate to cotton from other hosts, severe injury may cause plants to shed squares and small bolls. Generally, large populations develop after insecticide has been applied for control of other cotton pests.

APHIDS

Cotton aphid (also called melon aphid), *Aphis gossypii* Glover
Cowpea aphid, *Aphis craccivora* Koch
Green peach aphid, *Myzus persicae* (Sulzer)
Potato aphid, *Macrosiphum euphorbiae* (Thomas)

Species Attacking Cotton and Distribution—These aphids are nearly worldwide in distribution and are pests of seedling stage cotton throughout the Cotton Belt. The cotton aphid may persist throughout the season and is a particular threat to the crop when cotton bolls open (Anonymous, 1984b).

Identification and Development of the Stages—Adult and immature stages of the aphid species are similar in shape, but differ in size, color, and in relative size of the cornicles, cauda and last antennal segment. The cotton aphid (Plate 2-29), which is the most common pest species on cotton, is smallest at 3/64-1/16 inch (1.1-1.7 mm) long. Most commonly it is yellow or greenish-yellow in color, but may be brownish to almost dull greenish-black. The cowpea aphid is 2/32-5/64 inch (1.6-1.9 mm) long and shiny black. The green peach aphid is 1/16-5/64 in (1.8-2.1 mm) long, and green, pink or yellow in color. Cornicles (prominent tubules on top of the insect terminal end) of the cotton aphid are shortest and scarcely extend to or beyond the edge of the body, while on the cowpea and green peach aphids they are long and at least one half of their length extends beyond their body. The last antennal segment and the cauda (the tail) are shortest on the cotton aphid, and proportionately longer on the cowpea and green peach aphids. While winged forms occur, they usually are not common and their wing patterns are similar for the three species described. Color of the immature stages may be less intense than that of the adults, but is usually quite similar.

Invading winged and wingless adult aphids give birth to between two and three living nymphs each day. These nymphs appear very much like the adults. Nymphs can complete their development to the adult stage and begin reproduction in as little as four to six days and will produce about 50 offspring during their lifetime. Winged forms are produced when hosts become unfavorable.

Damage Symptoms—Aphids commonly infest the lower surfaces of developing terminal leaves of the mainstem and branches, causing them to become crinkled and to cup downward. When infestations are heavy, they also may colonize the tender stem tissue and the bracts of squares. Infestations are recognized best by the appearance of developing leaves and the shiny honeydew that they excrete onto the leaves below the infestation. In late season, when bolls begin to open, aphids excrete honeydew onto the fiber (Plate 2-30). This honeydew may stick to picker spindles, ginning equipment and spinning equipment at the mills, making harvest and processing of the fibers difficult or impossible. This greatly jeopardizes sale of the crop. Sooty molds may grow on the honeydew, causing discoloration of the fiber and reduced grade.

Infestations of aphids on seedling and small cotton plants may permanently stunt the growth and cause death of plants (Smith, 1942). The most significant reductions in

yield occur when young plants are infested, but yield reductions can result from later infestations (Smith, 1942; Isely, 1946)

Alternate Hosts—The cotton aphid has a wide range of hosts (Paddock, 1919). It is most commonly reported as a pest of cotton, hibiscus, melon, okra and squash and is also reported from citrus. While all of these hosts may develop large numbers of aphids, there is a degree of inter-host incompatibility (Isely, 1946; Swift, 1958). There is no clear verification of alternate host source contribution to outbreaks in cotton although this pest overwinters on citrus and a number of weed or wild non-cotton hosts.

Phenology and Population Dynamics—While winter eggs of the cotton aphid have been recorded in areas of its more northern distribution, it is capable of year-round reproduction on suitable hosts (Paddock, 1919) including dock, *Rumex* spp., and other winter weeds (Swift, 1958). Its rapid rate of development, high reproductive rate and low reproductive temperature threshold make infestation development highly volatile. While infestations of aphids may occur throughout the season, the three dominant aphid pests are most abundant in early spring and outbreaks of the cotton aphid frequently occur in late summer and fall.

Periodic outbreaks of aphids occur at periods of several years. At the present time, entomologists have not been able to develop a clear cause-and-effect relationship for these outbreaks. However, they occur over wide geographic areas on many crops and involve several aphid species.

Spring outbreaks of aphids, particularly the cotton aphid, appear to be a result of the capacity for this insect group to reproduce at temperature thresholds that are lower than the reproductive thresholds of their natural enemies (Isely, 1946). These and later season infestations are usually controlled by parasitic wasps and predators. During some years infestations will develop during September and October. This apparently is due to low population levels of several of their natural enemies which may result from the use of insecticides against other pests or the detrimental impact of a hyperparasite on numbers of the major aphid parasite, *Lysiphlebus testaceipes* Cresson. Fall outbreaks may also be due to onset of cooler weather.

Reproduction by the cotton aphid in the Cotton Belt is continuous throughout the year and there are no distinctive generations on cotton. The potential for invasion of and development on cotton appears to be regulated largely by temperature, since reproductive potential is greatest at about 68F (20C) and is reduced by hot summer weather. The threat of infestation development is then conditioned by numbers of natural enemies that may be present.

WHITEFLIES

Sweetpotato whitefly, *Bemisia tabaci* (Gennadius)
Silverleaf whitefly, *Bemisia argentifolii* Perring and Bellows
Bandedwinged whitefly, *Trialeurodes abutilonea* (Haldeman)
Greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood)
Aleyrodes spiraeoides (Quaintance)

Species Attacking Cotton and Distribution—The sweetpotato whitefly occurs worldwide. It was described from tobacco in Greece in 1889 (Mound and Halsey, 1978). Russell (1957) reported it as a serious pest of cultivated crops in Central America, South America, the West Indies, Africa and Asia. In the United States, sweetpotato whitefly became a serious pest of cotton in the low desert areas of Arizona and California where it cycled from cotton to fall and winter vegetables and back to melons and cotton again in spring and summer. In 1990 a more virulent whitefly, now referred to as the silverleaf whitefly (Plate 2-31) (Perring *et al.*,1993), appeared in the low desert regions of Arizona and California (Brown *et al.*, 1991; Costa and Brown, 1991) and appears to have displaced the sweetpotato whitefly. This new species (which is morphologically indistinguishable from the sweetpotato whitefly but genetically distinctive and with different biological characteristics), devastated several crops in the low desert and Lower Rio Grande Valley of Texas during 1991-92 and spread into the San Joaquin Valley of California.

The bandedwinged whitefly (Plate 2-32) occurs across the Cotton Belt of the United States and is most frequently reported as a pest of cotton in Louisiana and locally in the San Joaquin Valley of California. The greenhouse whitefly is a frequent pest and *Aleyrodes spiraeoides* is a localized pest of cotton in the San Joaquin Valley of California.

Identification and Development Stages—The sweetpotato and silverleaf whiteflies are tiny, 1/16 inch (1.6 mm), white, mothlike insects. The nymphs are entirely different from the adults. They are tiny and scale-like, flat and fringed with white waxy filaments. Gill (undated) has provided a key and color guide to identification of the pupal stage of these whitefly. The first stage is known as the crawler and moves about until settling down to feed. The immature stages are opaque with pale yellow spots within their body.They develop red eye spots in the pupal stage. They have piercing-sucking mouth parts, are confined to the underside of leaves, and secrete sticky honeydew (Plate 2-31). Whitefly eggs have a short subterminal stalk which the female inserts into the leaf tissue of the host plant, usually on the lower surface of a leaf (Mound and Halsey, 1978). Under high populations, hundreds of eggs can be found per square centimeter of leaf surface. Eggs are opaque when deposited and turn black within three days.

Adults begin feeding soon after emergence and mate within one to two days. Reproduction is arrhenotokous, i.e., unmated females produce male progeny. Under typical summer-time conditions the pre-oviposition period is one to two days. Eggs are laid singly on both the underside and top of the leaf, but usually on the underside unless populations are extremely high. Developmental rates vary, depending upon temperature (Butler and Henneberry, 1986) and host plant (Coudriet *et al.*, 1985). Gameel (1978) reported the incubation period on cotton to be 20.5 and 5.2 days at 60 and 104F (15 and 40C), respectively. Development from egg to adult at 80F (26.7C) ranged from 16 days on sweetpotato to the maximum time of 38 days on carrots (Coudriet *et al.*, 1985). Butler and Henneberry (1986) reported that adult longevity was

highly variable, depending upon temperature, ranging from 2 to 34 days in the male and 8 to 60 days in the female.

Damage Symptoms—Damage symptoms on cotton are two-fold. First, honeydew secretions by both the immature and adult stages cause a glossy, shiny appearance to the contaminated foliage. Foliage and lint in open bolls become sticky to the touch. Later, a blackening of foliage and lint may occur due to the growth of a sooty-mold fungus on the honeydew. The sweetpotato and silverleaf whiteflies are also vectors of a virus-like disease of cotton called cotton leafcrumple. This causes distorted and stunted growth of the terminal areas of the plant and, if infection occurs early in the life of the plant, will cause severe yield losses. The distortion of the terminal foliage is in the form of severely crumpled and discolored leaves (Allen *et al*., 1960). In addition to removing plant nutrients, whiteflies produce numerous chlorotic spots on infested leaves, by the action of the saliva of feeding adults as well as by the removal of cell contents by the immature stages. Under heavy feeding, the chlorotic areas coalesce and cause an irregular yellowing of the leaf tissue which extends from the veins to the outer edge of the leaf. The silverleaf whitefly is capable of killing cotton and other crop plants.

The honeydew excreted by all immature stages covers the leaves and may affect the metabolic processes. It can contaminate the seed cotton in open bolls (Plate 2-30) and create problems in harvesting, ginning and spinning (Gameel, 1977).

Alternate Hosts—Greenhouse, sweetpotato and silverleaf whiteflies have a wide range of crop, native plant and weed hosts in numerous plant families. While the host lists for the bandedwinged whitefly and *Aleyrodes spiraeoides* are much shorter than for the other species, host types are still numerous and varied.

Butler and Henneberry (1986) reported sweetpotato whitefly adults overwintering in the Phoenix, Arizona area on cheeseweed, *Malva parviflora* L., and prickly lettuce, *Lactuca serriola* L., during January and February 1982. Natwick and Zalom (1984) stated that although the sweetpotato whitefly has been reported in the desert southwest since the late 1920s, it first became a significant pest in both southern California and Arizona during 1981, when it inflicted serious damage to cotton, melon, squash, lettuce and sugarbeets. The potential for sweetpotato whitefly to overwinter on 17 cultivated crops grown in the southern California desert valleys was reported by Coudriet *et al*. (1985). In addition to the crops given above, these included: carrots, broccoli, tomato, flax, guar, pepper, guayule, bean, alfalfa, eggplant, cucumber and sweetpotato. Coudriet *et al*. (1986) reported 9 weed hosts on which sweetpotato whitefly development could be completed. These were: wild sunflower, *Helianthus annuus* L.; mesquite, *Prosopis* spp.; malva, *Malva parviflora* L.; horseweed, *Conyza canadensis* (L.) Cronq.); field bindweed, *Convolvulus arvensis* (L.); Wrights' ground cherry, *Physalis acutifolia* (Miers) Sandwith.; common sowthistle, *Sonchus oleraceus* (L.); spring sowthistle, *Sonchus asper* (L.) Hill; and wild lettuce, *Lactuca serriola* L. Mound and Halsey (1978) reported 315 plant species as hosts of sweetpotato whitefly.

These reports indicate the extensive host range of the sweetpotato and silverleaf

whitefly and thus the difficulty in achieving control culturally by breaking the cycle through host-free periods. It is fortunate that many of these hosts are relatively scarce and untreated and thus, help maintain the reservoir of parasites which can be so effective in the control of the whitefly.

Phenology and Population Dynamics—Whiteflies are tropical and subtropical insects that must reproduce throughout the year. Their numbers drop to very low levels during winter when hosts may be scarce and weather is adverse. The sweetpotato whitefly is trapped throughout the year in the Imperial Valley of California and the Yuma area of Arizona (Watson *et al.*, 1992). Infestations on cotton develop slowly during spring although whiteflies may be found on cotton by April. Highest densities are attained during August through October. This coincides with cotton boll opening. Bandedwinged whitefly is often detected by mid-July in Louisiana and reaches maximum infestation levels when cotton bolls are opening in late-August through September. In western Arizona the bandedwinged whitefly predominated during the earlier part of the season, with nearly total displacement by the sweetpotato whitefly by late-June to early-July (Watson *et al.*, 1992). While this species may be trapped throughout the year in the California San Joaquin Valley, it is usually detected locally in cotton fields during mid- and late-summer. The greenhouse whitefly is also trapped throughout the year in the San Joaquin Valley where population numbers increase rapidly with onset of hot summer weather. Like the other species, infestation levels usually become highest during August through October.

The extensive host range, effect of both temperature and plant host on developmental rate, biological control agents and grower management practices, particularly chemical control, contribute to the complex ecology of the sweetpotato whitefly. Under certain conditions in Arizona and California cotton fields, Butler *et al.* (1985) found that populations doubled every six to ten days. These factors should similarly affect the other species.

Whitefly populations are characterized by rapid increase and intercrop movement in multicrop agricultural systems (Horowitz *et al.*, 1982). This occurs in spite of high natural mortality during the crawler stage and first larval instar. The distribution of whitefly within the plant canopy on the underside of leaves, as well as their high reproductive potential, contribute to the difficulty in controlling the insect with conventional spray application methods (Butler and Henneberry, 1986). Fullerton (1982) found nymphal reductions of 83.1, 33.2 and 22.5 percent respectively, from terminal, mid-plant and bottom leaves, 24 hours after treatment.

The role of natural enemies in regulating sweetpotato whitefly populations is unknown. However, outbreaks appear to intensify with the use of synthetic organic insecticides, suggesting that natural enemies play a significant role in population regulation (Anonymous, 1981). Gerling (1967) reported that whiteflies in southern California seldom reached economic levels except when insecticide applications were applied to cotton. He suggested that natural regulating factors were important in maintaining low population levels.

In regions of the San Joaquin Valley during many years, the parasitic wasp, *Eretmocerous haldemani* Howard and a complex of predacious insects appear to provide effective control of the greenhouse and bandedwinged whitefly.

THRIPS

Flower thrips, *Frankliniella tritici* (Fitch)
Western flower thrips, *Frankliniella occidentalis* (Pergande)
Frankliniella exigua Hood
Frankliniella gossypiana Hood
Tobacco thrips, *Frankliniella fusca* (Hinds)
Onion thrips, *Thrips tabaci* Lindeman
Soybean thrips, *Sericothrips variabilis* (Beach)
Bean thrips, *Caliothrips fasciatus* (Pergande)
Caliothrips phaseoli (Hood)
Kurtomathrips morrilli Moulton

Species Attacking Cotton and Distribution (Anonymous, 1984a)—The flower, western flower and onion thrips occur throughout the Cotton Belt as well as elsewhere in the United states. The onion thrips apparently occurs worldwide wherever onions are grown. The western flower thrips is reported in greenhouses in Europe and on outdoor plants in many other countries. Locally, either of these two species may predominate in a particular year, although the western flower thrips appears to be the most general pest. Other species appear to be localized in their distribution. The bean thrips is reported to occur in the western and southeastern United States as well as in Mexico and South America.

Identification and Development of the Stages—Adult females of the flower, western flower (Plate 2-33) and onion thrips are predominantly straw colored although intermediate to dark brown color forms occur (Metcalf *et al.*, 1962; Bryan and Smith, 1956). The same color forms may occur in the other species. Adult females are about 1/12th inch (1.5-2 mm) long, and have four wings that fold over their backs and are fringed with long hairs. Males are wingless and very rare. First instar nymphs usually are pale to ivory and second instar nymphs golden yellow in color and resemble the adults in shape. Eggs, which usually are deposited within the leaf tissue, are reniform and usually can be located by staining the plant tissue and examining it with the aid of strong magnification (Bryan and Smith, 1956).

Adult bean thrips are about 1/25th inch (5 mm) long, slender and black with white bands across the wings which fold on the dorsum of the abdomen. The first instar nymphs are slender, pale to dark orange in color, and resemble the adults in shape. Older nymphs have deep pink to orange spots on the abdomen (Smith, 1942).

Thrips develop through the egg, two nymphal stages and the propupal and pupal stage before becoming adults. The egg stage lasts from three to four days during hot summer weather to two weeks or more in colder winter and spring weather. First and second instar nymphs complete their development in 2 to 10 and 3.5 to 12 days,

respectively, depending on temperature. Fully developed nymphs drop to the soil to pupate. The pupal stage may be as short as four days. Total development time is as little as two weeks. Adult females live about a month and deposit 40 to 50 eggs during their lifetime. While males are rare, their development is very similar to that of females and they are smaller (Bryan and Smith, 1956).

Damage Symptoms—The flower thrips, western flower thrips and onion thrips are most frequently reported as pests of seedling cotton, particularly where cotton is grown at higher elevations and cool temperatures persist. The western flower thrips is reported to be a mid-season pest of cotton in Arkansas, Louisiana, Georgia and Mississippi. The bean thrips is an infrequent mid-season pest in the San Joaquin Valley of California.

Thrips feed on the surface of the plant tissue. They pierce the epidermal cells with needle-like stylets and suck the plant liquids. Their very small size permits them to crawl into the folded terminal leaves. With the exception of the bean thrips, most species demonstrate a preference for feeding within the folded developing leaves in the plant growing points, in folds of leaves or at the base of leaf veins and in spider mite colonies. Spotted silvering on the lower surfaces of cotyledons and leaves is a typical result of their feeding. During severe outbreaks thrips feeding in the growing points will cause severe deformation and stunting of the developing leaves. The growing point may be completely destroyed in some instances. Death of plants is uncommon but can occur with continued severe attack. When plant terminals are destroyed, new buds must be initiated and bloom may be delayed for about two weeks (Smith, 1942).Thrips will continue to feed on cotton plants throughout the growing season. Immature stages are commonly found on lower leaf surfaces, particularly within spider mite colonies, while adults are found within blooms feeding on pollen.

With the onset of hot weather, cotton plants injured during the seedling stage outgrow thrips injury and develop normal leaves. Severely injured plants that loose apical terminals develop vegetative branches from mainstem nodes and become candelabra shaped with three to five terminals (Race, 1965).

The bean thrips typically attacks more mature leaves of cotton plants, feeding on the lower leaf surfaces where they cause the typical spotted silvering. Their excrement spots will also be very evident in feeding areas. These leaves will attain a copperish color, turn brown and fall from the plants. Squares and small bolls will also abscise. The tendency for leaf abscission suggests injection of a plant toxin during their feeding process (Smith, 1942).

Alternate Hosts—Flower, western flower and onion thrips have many hosts in the areas where they occur. These include grasses, cereal grains, alfalfa and other leguminous crops, numerous broad leafed plants in several plant families and a number of field and vegetable crops. Large populations often develop on these hosts, particularly on alfalfa, and migrate into cotton during the early seedling stage of crop development (Bailey, 1938; Newsom *et al.*, 1953; Race, 1965). In the Mid-South, large numbers of the western flower thrips apparently develop on grain crops and migrate to cotton dur-

ing the early flowering stage, where they feed on the blooms.

Phenology and Population Dynamics—In colder regions of the Cotton Belt adult thrips overwinter in fine-textured plant litter (Race, 1965) while, in the warmer areas such as Louisiana and California, they may reproduce on suitable hosts throughout the year (Smith, 1942; Newsom *et al.*, 1953). Large numbers develop on uncultivated hosts as well as on winter and spring grown cereal grains, alfalfa or clover crops. Greatest numbers may occur on cotton in late spring and early summer as the native vegetation matures and dries. However, they may be abundant in blossoms throughout the spring and summer. While the most evident damage to cotton occurs in the seedling stage, greatest numbers of thrips are present when the plants are in bloom. However, blooming plants can usually tolerate these numbers without obvious damage. In portions of Arkansas, Mississippi and Louisiana, the western flower thrips may reach greatest numbers on cotton in early July when maturation of grain crops occurs.Weather conditions that provide an abundance of natural annual vegetation during late winter and spring and extensive plantings of cereal grains can lead to high populations of thrips. Continued rainfall during the cotton growing season and sprinkler irrigation may seal the soil where the thrips pupate and can prevent their emergence as adults. Cool weather that slows plant growth during the seedling stage enhances the severity of thrips injury. However, cotton plants usually outgrow thrips damage when they are about 32 days old (Race, 1965).

SUMMARY

The most frequently encountered insect and spider mite pests of cotton are reviewed. While the several species in each group are cited, only the most common pest species and their damage are described. Geographic distribution, phenology, population dynamics, population regulation by natural enemies and host contributions to outbreaks are reviewed. References cited in the text will provide details of the cited information and will serve as a guide to extensive literature on the the various topics.

ACKNOWLEDGMENTS

We are grateful to the University of California Statewide IPM Project and photographer Jack Kelly Clark for approval to use 31 photographs of cotton insects and their damage. These pictures are taken from Integrated Pest Management for Cotton in the Western Region of the United States, University of California Division of Agriculture and Natural Sciences Publication 3305. Winfield L. Sterling, Texas A&M University has kindly provided photographs of the cotton leafworm moth and larvae, and Michael J. Gaylor of Auburn University has provided a graph of tarnished plant bug host contributions to outbreaks of that pest. Other graphs are by the senior author of this chapter, Thomas F. Leigh.

Chapter 2

APPENDIX

IDENTIFICATION AND DAMAGE GUIDE TO PEST INSECTS AND MITES

The information and color plates that follow are intended to aid readers in identification of insect injury observed in cotton fields and in identification of insects and spider mites they see and examine. Color plates of the most common pests are included. The user of this identification guide is also referred to Chapter 3 for descriptions of the beneficial natural enemies of cotton pests.

More than 100 insect and spider mite species may be found in cotton fields. While a few of these species appear in damaging numbers annually, many are rare in their occurrence and others are predators or parasites of the pests.

Effective control, environmental concerns associated with insecticide use, disruption of natural biological control systems and costs of insecticides and their application dictate that the cotton grower or his crop advisors carefully ascertain which pest(s) must be controlled. Few insecticides are effective against a wide range of these pests and use of the wrong material may result in control failure in addition to outbreaks of other pests against which they are not effective. Management of insect and mite pests depends very much on their proper identification, an understanding of their interrelationships, and knowledge of the threat they pose to the crop.

Particular pests will usually dominate in the type of management strategy selected for a particular region of the Cotton Belt. Need for control of thrips, boll weevils and lygus bugs frequently will dominate pest management decisions in states east of Texas and Oklahoma. In Texas and Oklahoma, fleahoppers, boll weevils and thrips may be the most frequent pests. In the far west, lygus bugs, pink bollworms and whiteflies are often the earliest seasonal targets. Aphids and the threat of sticky cotton have become increasingly significant across the Cotton Belt.

Both a cotton insect/mite pest species (types) identification guide and an insect/mite damage symptoms guide are included in this chapter appendix. Pest types are grouped according to physical characteristics that are most apparent. Damage symptoms are grouped by stage of growth and development of the cotton plant.

INSECT AND MITE DAMAGE IN COTTON

(Major Pests in Bold Type)

Many insects are referenced to the color plates that follow.

	DAMAGE SYMPTOMS	PEST	PLATE
PLANTED SEEDS			
Seeds	eaten. Stand poor.	seedcorn maggot wireworms	not incl.
SEEDLINGS			
Stems	cut off just above or just below ground level.	cutworms	not incl.
	gouged at or above ground level.	darkling beetles field crickets	not incl.
Stems, Cotyledons, Leaves	dried and shriveled.	false chinch bugs	not incl.
Cotyledons, Leaves	covered with honeydew.	aphids	not incl.
	silvery, without honeydew.	thrips	not incl.
	ragged, eaten.	**beet armyworm** alfalfa looper field cricket	not incl.

ESTABLISHED PLANTS

Stems	with rows of deep gouges.	cicada egg punctures (rare).	not incl.
Leaves	bored into or cut off near terminal.	**beet armyworm**	not incl.
	covered with honeydew, deformed.	aphid	not incl.
	not deformed.	whitefly	not incl.
	discolored above, usually webbed beneath.	spider mites	Plate 2-19
	not webbed, veins distorted	potato leafhopper	Plate 2-28
	with twisting mines and windows or holes	cotton leafperforator	Plate 2-25
	and no holes.	leafminer	not incl.
	skeletonized, with twisting mines.	cotton leafperforator	Plate 2-25
	by small caterpillars	**beet armyworm**	Plate 2-16
	feeding in a group.	fall armyworm	
		yellowstriped armyworm	
		saltmarsh caterpillar	
		cotton leafworm	
	ragged, eaten; caterpillars present.	**beet armyworm**	not incl.
		cabbage looper	Plate 2–21
		soybean looper	
		yellowstriped armyworm	
		saltmarsh caterpillar	
		cotton leafworm	Plate 2–22

INSECT AND MITE DAMAGE IN COTTON (Continued)

	DAMAGE SYMPTOMS	PEST	PLATE
Leaves	ragged, eaten; insects present (not caterpillars)	cucumber beetles field crickets grasshoppers	not incl.
	rolled and webbed, terminal leaves eaten.	omnivorous leafroller	not incl.
	older leaves rolled and webbed.	celery leaftier	not incl.
Squares	small hole eaten in side, may be plugged with excrement, flared, dropped.	**boll weevil**	Plate 2-2
	punctured, flared, dropped, shiny spots of excrement. Also, very small squares dried in plant terminal.	**lygus bugs** fleahoppers superb plant bug clouded plant bug	Plate 2-12
	without excrement spots.	**stink bugs**	not incl.
	eaten into, dropped.	**beet armyworm** **bollworm** **tobacco budworm** fall armyworm yellowstriped armyworm cotton square borer **boll weevil**	not incl.

	with bracts chewed, and webbed.	omnivorous leafroller	not incl.
Blooms	with rosetted petals.	**pink bollworm**	not incl.
	with hole eaten out of base.	**beet armyworm** **bollworm** **tobacco budworm** fall armyworm yellowstriped armyworm cotton square borer	not incl.
	disfigured, warty.	**lygus bug** superb plant bug clouded plant bug	not incl.
Bolls	with slightly depressed reddish brown spots, shiny excrement spots, small bolls drop.	**lygus bug** clouded plant bug superb plant bug	not incl.
	without excrement spots, may crack and show internal rot.	**stink bug**	not incl.
	with hole in side, eaten out, small bolls may drop.	**beet armyworm** **bollworm** **tobacco budworm** fall armyworm yellowstriped armyworm	not incl. Plate 2-4

INSECT AND MITE DAMAGE IN COTTON (Continued)

	DAMAGE SYMPTOMS	PEST	PLATE
Bolls	bored at tip, chewed.	cotton leafperforator omnivorous leafroller	not incl.
	with holes through wet lint and walls separating locs.		
	pink larvae in seeds of large bolls.	**pink bollworm**	Plate 2-8
	white larvae in holes in lint.	**boll weevil**	not incl.
	open and normal but honeydew and mold on lint.	aphids whitefly	Plate 2-30 Plate 2-30

FIELD GUIDE TO COMMON INSECT AND MITE PESTS OF COTTON

(Major Pests in Bold Type)

INSECT EGGS	DESCRIPTION	PEST	PLATE
Laid in groups or clusters.	Pale green, usually on upper leaf surface beneath top canopy. Covered with velvety moth scales.	**beet armyworm** fall armyworm yellowstriped armyworm	Plate 2-15
	Pale bluegreen, flat, overlapping on upper leaf surfaces.	omnivorous leafroller leaf tiers	not incl.
	Pearl-like, spherical, not covered. Usually on upper leaf surface near top of plant.	saltmarsh caterpillar	not incl.
	White to gray, like closely stacked barrels, in clusters of 7, 14 or 28.	**stink bugs**	Plate 2-14
Laid singly.	White, with brownish band in upper third soon after deposition. On terminals & squares. As tall as wide at base.	**bollworm** **tobacco budworm**	Plate 2-3
	White, without brownish band, shorter than wide at base. Laid on under side of leaves below terminal.	**cabbage looper** alfalfa looper	Plate 2-23
	Blue-green to dirty white. Dish shaped. Circular, flattened, ribbed. On lower leaf surface middle third of plant.	cotton leafworm	not incl.

FIELD GUIDE TO COMMON INSECT AND MITE PESTS OF COTTON (Continued)

	DESCRIPTION		PEST	PLATE
Laid singly	Greenish to red, oval, laid at bases of bolls and on inside of bracts.		**pink bollworm**	not incl.

CATERPILLARS

(Larvae of moths and butterflies. Have false legs on abdomen in addition to the three pairs of legs on the thorax.)

Exposed on foliage	Body almost concealed by long yellow to black hair. To 1 1/4 inches.		saltmarsh caterpillar	
	Body naked	Only two pairs of false legs, behind middle of abdomen. Pale green, walk as "loopers". Length to 1 1/4 inch.	**cabbage looper** alfalfa looper	Plate 2-21
		3 pairs of hind legs, yellowish green with narrow white strips, distinctive spots on dorsum. Semiloopers. Length to 1 1/2 inch.	cotton leafworm	Plate 2-22
		Skin smooth. Dull green with black spots and white bumps. Length to 3/8 inch; slender.	cotton leafperforator	Plate 2-26

			Greenish with dusky stripe down side, tiny black spot above middle true leg. Length to 1 inch.	**beet armyworm**	Plate 2-17
			Black with yellow and and brown stripes. Length to 1 1/4 inch.	yellowstriped armyworm	not incl.
			Brown with darker bumps on back, pale inverted "Y" on head. Length to 1 1/4 inch.	fall armyworm	not incl.
On or in boll (sometimes blossom or square)	No visible entrance hole in boll, but sometimes frass-free exit hole. Tiny white to 1/2-inch pink caterpillar in lint or seed, often mines or warts in inner carpel walls & holes in lock separators.			**pink bollworm**	Plate 2-8
	Slight feeding at tip of boll. Dull green caterpillar with black spots & white bumps, 3/8 inch.			cotton leafperforator (rare)	not incl.
	Hole in side of boll	Skin of body with tiny spines.	Greenish to rose brown with irregular black stripes. Length to 1 1/4 inch.	**bollworm** **tobacco budworm**	Plate 2-4

FIELD GUIDE TO COMMON INSECT AND MITE PESTS OF COTTON (Continued)

DESCRIPTION			PEST	PLATE
	Skin without spines.	Smooth, greenish with dusky stripe down side and tiny spot above middle true leg. Length to 1 inch.	**beet armyworm**	Plate 2-17
		Smooth, black with yellow and brown stripes. Length to 1 1/4 inch	yellowstriped armyworm	not incl.
		Brown with darker bumps on back, pale inverted "Y" on head. Length to 1 1/4 inch.	fall armyworm	not incl.
		Velvety green, with dense coat of short, erect hairs. Head small. Length to 3/8 inch.	cotton square borer (rare)	not incl.
Within webbed or rolled leaves or bracts. Olive green, with white spots or spines on each segment. Crawl forward or backward rapidly. Length to ½ inch.			omnivorous leafroller leaftiers	not incl.

	Within leaf mines. Tiny, to 1/16 inch, white.	**cotton leafperforator**	Plate 2-25
	In soil near severed seedlings. Mottled gray to brown, greasy, shiny. Curl up when disturbed. Length to 1 inch.	cutworms	not incl.
OTHER LARVAE			
With distinct head	In wet lint in boll. C-shaped, cream with tan head, legless. Length to 3/8 inch.	**boll weevil**	not incl.
Maggots (head end tapering)	White to cream, length to 3/8 inch. In soil, in seed, or on underground parts of damaged seedlings.	seedcorn maggot	not incl.
	Tiny, white, with black mouth hooks at front end. In leaf mines. Length to 1/8 inch.	leaf miner	not incl.
COCOONS AND PUPAE			
Loose or flimsy white cocoon	3/4 inch long, enveloping a green caterpillar or brown pupae.	**cabbage looper**	not incl.
	Brown to near black pupae to near 13/16 inch. In fold of leaf.	cotton leafworm	not incl.
	1/4 inch long, enveloping a U-shaped larva. Horseshoe stage of...	**cotton leafperforator**	not incl.

FIELD GUIDE TO COMMON INSECT AND MITE PESTS OF COTTON (Continued)

		DESCRIPTION	PEST	PLATE
		Found in leaf trash or near base of plant, pink larvae or brown velvety pupae to 2/5 inch long.	**pink bollworm**	not incl.
Tight tapered white cocoon		1/4 inch long with fine ridges. Cocoon of...	**cotton leafperforator**	not incl.
TRUE BUGS				
Mouth parts a sucking beak.				
Triangular shaped, wings membranous, held roof like over abdomen. 1/8 inch long.			leafhoppers	Plate 2-27
Wings held flat on back, leathery at base, membranous beyond middle, wings and the triangular scutellum forming an "X" on the back.				
1/4 inch long or longer.	Shield shaped	1/4 to 1/2 inch long, green to brown. Some species with pointed shoulders.	**stink bug**	Plate 2-13
	Oval in outline	1/4 inch, greenish with yellow heart-shaped mark on scutellum, wings often reddish to brown near middle.	**lygus bug**	Plate 2-9

	3/8 inch, mostly black, margined with orange or red.	superb plant bug	not incl.
	9/32 inch long, yellowish tan to brown.	clouded plant bug	not incl.
1/8 inch long or less	Pale green with black specks on body.	cotton fleahopper	Plate 2-11
	Black with base of leathery part of front wing brownish. Last two antennal segments white.	western plant bug	not incl.
	Black with white marking on leathery part of front wings. Antennae entirely black.	whitemarked fleahopper	not incl.
	Aggregate in large numbers. Feed early morning, late evening. Hide beneath clods of dirt in daytime.	false chinch bug	not incl.
BEETLES			
Wing covers with dark markings	1/4 inch, soft bodied: green to yellowish; wing covers with black spots or stripes.	cucumber beetles	not incl.
	3/16 inch. Tan with yellow stripe down each wing cover. Hind legs thickened for jumping.	flea beetle	not incl.

FIELD GUIDE TO COMMON INSECT AND MITE PESTS OF COTTON (Continued)

	DESCRIPTION	PEST	PLATE
Wing covers one-colored	Front of head drawn out into a curved snout. 1/4 inch, tan to brown. Femur of front leg with large double tooth.	**boll weevil**	Plate 2-1
	1/4 inch. Dull brown to black. In soil near seedlings with gouged stems.	darkling beetle	not incl.
	3/16 inch, black, slender, tapered. Wing covers very short. In blossoms.	fruit bud beetle	not incl.
MOTHS (Only distinctive species that are likely to be seen in cotton fields are included.)			
3/4 inch long or longer	1 1/4 inch long. Wings white with black spots, male hind wings rich yellow. Top of abdomen orange & black.	saltmarsh caterpillar	not incl.
	3/4 inch long, variegated black & brown, front wing with a silver "Y" or gamma mark in middle. Thorax with tuft of long scales.	**cabbage looper** **soybean looper** alfalfa looper	not incl.
	3/4 inch long. Greenish tan, front wings with 3 diagonal darker bands, hind wings paler with outer third all black.	**tobacco budworm**	Plate 2-5

	3/4 inch long. Front wings rich tan with some browner pattern, hind wings paler with outer third black but enclosing pale spots.	**bollworm**	Plate 2-6
	3/4 inch long. Olive-tan color with three wavy transverse bars on front wings.	cotton leafworm	Plate 2-20
Less than 1/2 inch long	1/4 inch long, Very slender, all white.	**cotton leafperforator**	Plate 2-24
	3/8 inch long. Dark, triangular, with long snout.	omnivorous leafroller	not incl.
	Mottled grayish-brown moth.	**pink bollworm**	Plate 2-7
	Slender, variously yellowish to buff or reddish, with snout.	webworms	not incl.

OTHER INSECTS WITH OBVIOUS WINGS

Front and hind wings unequal.	Large, over 1 inch long, brown to black. Hind legs thickened for jumping. Antennae very long & slender.	field cricket	not incl.

FIELD GUIDE TO COMMON INSECT AND MITE PESTS OF COTTON (Continued)

	DESCRIPTION	PEST	PLATE
	Small, 1/8-1/4 inch, green to brown. Hind legs used in jumping.	leafhopper	Plate 2-27
	Small, to 1/8 inch, green to black, in colony with wingless individuals. Abdomen with 2 tubes (cornicle) at back.	**aphid**	Plate 2-29
	Tiny mothlike, 1/16 inch. Wings and body covered with white powder. Cloud of adults will fly. Adult...	**whitefly**	Plate 2-31 Plate 2-32
Only front wings present	1/16 inch long. Body black with yellow markings. Adult...	leafminer	not incl.
APPARENTLY WINGLESS INSECTS AND MITES			
1/8 to 1/4 inch long	Length to 1/8 inch, yellow to green to black. Abdomen with 2 tubes. Live in colonies. Produce honeydew.	**aphids**	Plate 2-29
	Length to 3/16 inch. Red antennae, green with black spot on abdomen, 4 black spots on older nymphs, varying to brownish, Active. Nymphs...	**lygus bug**	Plate 2-10

	Length to 1/4 inch, some larger, nearly circular. Green to brown with scent gland at middle of abdomen. Nymph...	**stink bug**	not incl.
Tiny 1/16 inch smaller	Flat, almost transparent, not obviously motile, usually with fringe of white waxy filaments. Produce honeydew. Nymphs...	**whitefly**	Plate 2-31 Plate 2-32
	Globular, in webbing on under side of leaves. Body not segmented, with four pairs of legs.	**spider mites**	Plate 2-18
	Slender, tapered at both ends. Active. Opaque to tan to dark.	larval thrips	Plate 2-33

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The authors acknowledge that the damage symptoms guide is adopted from "Arizona Cotton Insects", Cooperative Extension Service, University of Arizona, Bulletin A23 (Revised 1979). The authors of this bulletin are Floyd G. Werner, Leon Moore and Theo F. Watson.

Plate 2-1. Adult boll weevil, *Anthonomus grandis grandis* Boheman. (Adult commonly found beneath the bracts of squares or feeding in flowers during the day.)

Plate 2-2. Cotton square with a boll weevil, *Anthonomus grandis grandis* Boheman, egg puncture. (After ovipositing, adult weevil seals the feeding puncture with a frass plug.)

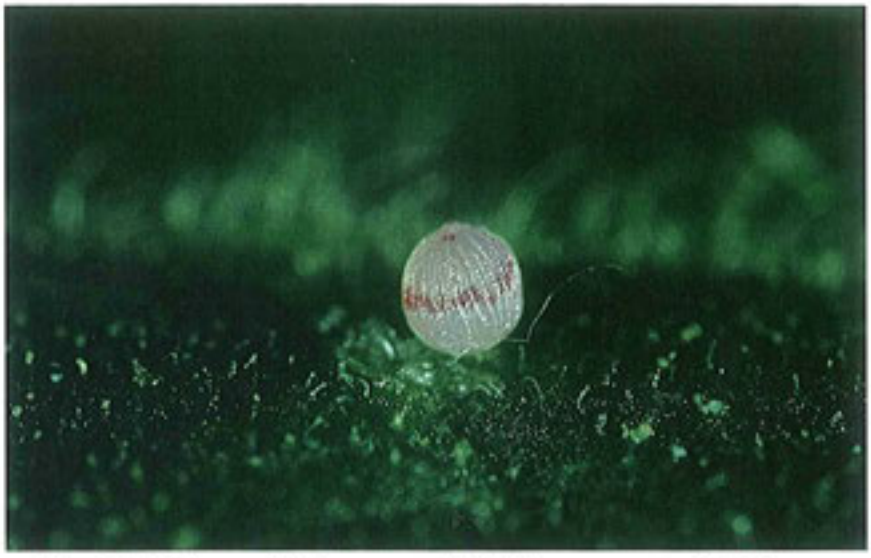

Plate 2-3. Bollworm, *Helicoverpa zea* (Boddie), egg on cotton leaf. (Egg develops a reddish brown ring a day after it is laid.)

Plate 2-4. Larvae of bollworm *Helicoverpa zea* (Boddie). (Under magnification, larva has tiny spines on most parts of the body and prominent tubercles.)

Plate 2-5. A mating pair of tobacco budworm, *Heliothis virescens* (F.), adults. (Illustrates the three oblique dark bands on the forewings and typical olivegreen color.)

Plate 2-6. Mating pair of pale buff colored bollworm, *Helicoverpa zea* (Boddie), moths.

Plate 2-7. Moth of the pink bollworm, *Pectinophora gossypiella* (Saunders).

Plate 2-8. Mature larva of the pink bollworm, *Pectinophora gossypiella* (Saunders), and associated cotton boll damage. (The first three larval stages are white, with a dark head capsule; the fourth stage shows pink coloring.)

Plate 2-9. Adult western lygus bug, *Lygus hesperus* Knight. (Illustrates the prominent heart-shaped scutellum, which is commonly yellow in this species.)

Plate 2-10. Nymphal western lygus bugs, *Lygus hesperus* Knight. (Nymphs are commonly green, with red antennal tips. Older nymphs have five black dots on the back and may be brownish in color.)

Plate 2-11. Nymphal and adult cotton fleahoppers, *Pseudatomoscelis seriatus* (Reuter). (Light green in color, speckled with small brown spots and numerous short spines, and have bristle-like antennae that are not reddish as in lygus bugs.)

Plate 2-12. Shriveled dried squares injured by western lygus bugs, *Lygus hesperus* Knight. (Often found in the plant terminals, or in the sweep net when sampling for this pest.)

Plate 2-13. Adult Say stink bug, *Chlorochroa sayi Stål.*

Plate 2-14. Egg mass of the consperse stink bug, *Euschistus conspersus* (Uhler).

Plate 2-15. Egg mass of the beet armyworm, *Spodoptera exigua* (Hübner) (Eggs usually laid on the upper leaf surface beneath the uppermost plant canopy and covered with white hair-like scales from the female moth's body.)

Plate 2-16. Young beet armyworm, *Spodoptera exigua* (Hübner), larvae (Usually feed in a group near where the eggs were laid, skeletonizing the leaf; often spin silk over the feeding site.)

Plate 2-17. Beet armyworm, *Spodoptera exigua* (Hübner) (Usually have a black spot on the side of the body above the second true leg. Color may vary from green to very dark green or black with lighter stripes on the sides of the body.)

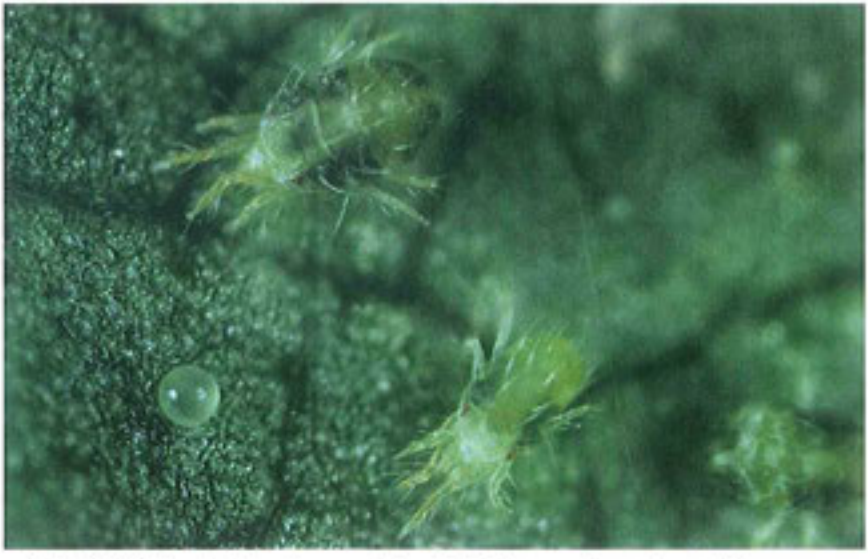

Plate 2-18. Female strawberry spider mite, *Tetranychus turkestani* Ugarov and Nikolski: immature stage and an egg. (The large dark body spots are typical of several spider mite species, although the adult carmine, *Tetranychus cinnabarinus* (Boisduval), and desert spider mites, *Tetranychus desertorum* Banks, are carmine and red in color, respectively.)

Plate 2-19. Spider mite damage symptoms. (Reddening of the leaves in small to large areas of fields and defoliation.)

Plate 2-20. Moth of the cotton leafworm, *Alabama argillacea* (Hübner). (Shows typical olive-tan color and three wavy transverse bars on the forewings.)

Plate 2-21. Larva of the cabbage looper, *Trichoplusia ni* (Hübner). (Alfalfa looper is similar in appearance.)

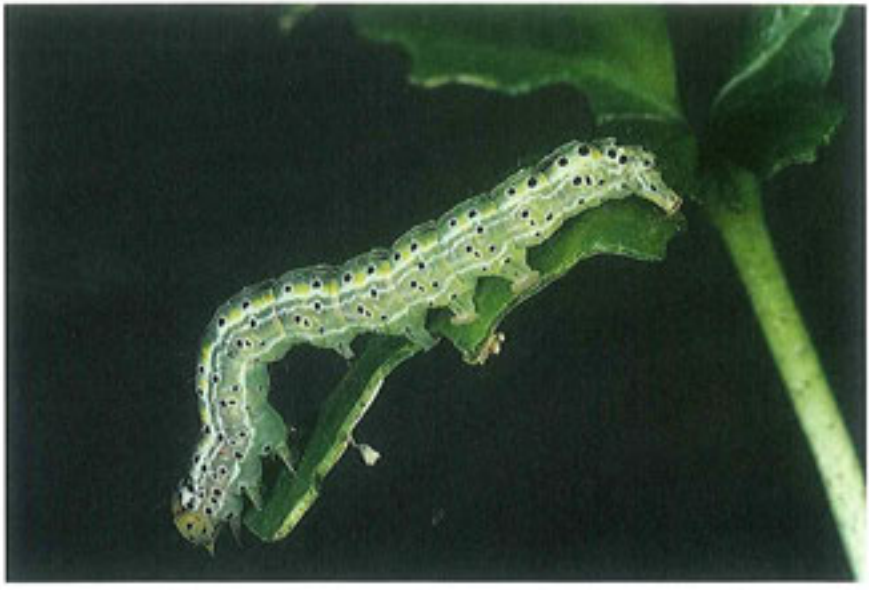

Plate 2-22. Cotton leafworm, *Alabama argillacea* (Hübner). (Illustrates distinctive white rings on the dorsum.)

Plate 2-23. Egg of the cabbage looper, *Trichoplusia ni* (Hübner). (Usually laid on the more mature leaves and is more flattened than bollworm eggs.)

Plate 2-24. Adult cotton leafperforator, *Bucculatrix thurberiella* Busck.

Plate 2-25. Cotton leafperforator, *Bucculatrix thurberiella* Busck, damage symptoms (mines) made by young larvae.

Plate 2-26. Fifth-instar cotton leafperforator, *Bucculatrix thurberiella* Busck, larva. (Fourth- and fifth-instar larvae skeletonize leaves.)

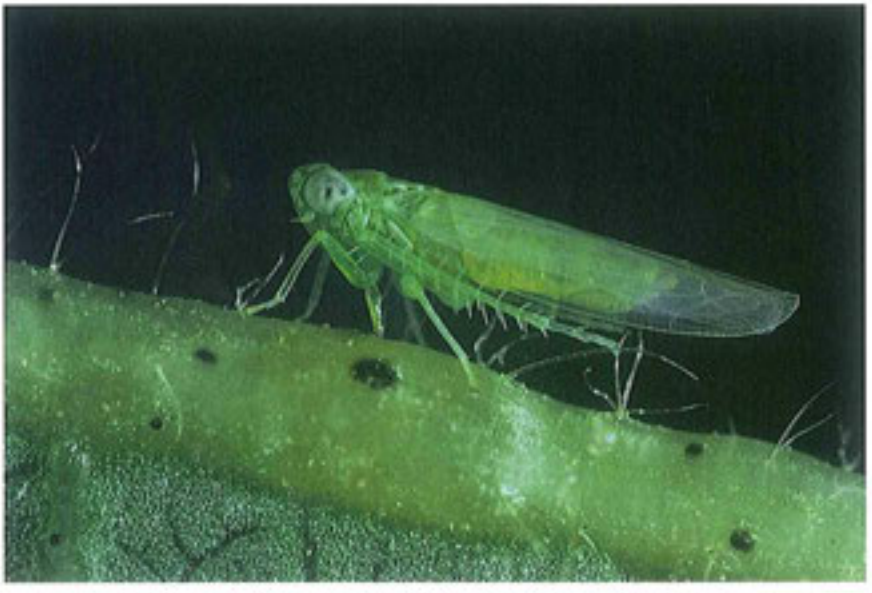

Plate 2-27. Potato leafhopper, *Empoasca fabae* (Harris), feeding on a leaf vein. (Feeding by this species and the southern garden leafhopper, *Empoasca solana* DeLong, causes veins to become swollen and rough.)

Plate 2-28. Potato leafhopper, *Empoasca fabae* (Harris), damage symptoms. (Cotton leaf illustrating cupped crumpling and discoloration.)

Plate 2-29. Colony of cotton aphid, *Aphis gossypii* Glover, on a lower leaf surface. (Shows light and dark forms of the aphid as well as winged and wingless types.)

Plate 2-30. Honeydew contaminated lint. (Honeydew excreted by aphids and whiteflies supports growth of sooty mold.)

Plate 2-31. Silverleaf whitefly, *Bemisia argentifolii* Perring and Bellows. [This species cannot be distinguished from the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), or the iris whitefly, *Aleyrodes spiraeoides* (Quaintance) except in the pupal stage.]

Plate 2-32. Bandedwing whitefly, *Trialeurodes abutilonea* (Haldeman). (Illustrates dark bands on the wings of adults. Immature stages of this pest are also evident.)

Plate 2-33. Adult of the western flower thrips, *Frankliniella occidentalis* (Pergande).

Chapter 3

BIOLOGY AND ECOLOGY OF IMPORTANT PREDATORS AND PARASITES ATTACKING ARTHROPOD PESTS

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INTRODUCTION

The important influences of natural enemies on cotton pests have been recognized for a long time (Quaintance and Brues, 1905; Whitcomb, 1971). However, their role in suppression of pest populations was not clearly recognized until, with widespread use of broad-spectrum insecticides, pest resurgence and secondary pest outbreaks were observed (Newsom and Brazzel, 1968).

Considerable research has been conducted to determine what species of natural enemies are important and how these can be used more effectively in cotton insect pest management. Although both vertebrate and invertebrate natural enemies prey on or parasitize the large number of arthropod pests of cotton, the emphasis here will be on predaceous and parasitic arthropods because they probably cause the most pest mortality (Sterling *et al.*, 1989). Some phytophagous (feed on plants) pests also prey on other pests of cotton. These include the cotton fleahopper, *Pseudatomoscelis seriatus*

(Reuter) (McDaniel and Sterling, 1982) (Plate 3-1[1]) and the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) (Cleveland, 1987). The biology and ecology of these are discussed in Chapter 2 (this book) by Leigh *et al.*

An estimated 300 to 600 species of arthropod natural enemies are found in cotton fields (Whitcomb and Bell, 1964; van den Bosch and Hagen, 1966). Of those, 15 or 20 are key species in the suppression of bollworm, *Helicoverpa zea* (Boddie), and tobacco budworm, *Heliothis virescens* (F.), in cotton (Ridgway and Lingren, 1972), and relatively few species would be added to this number if the entire pest complex of cotton were considered. The emphasis in this chapter will be on the biology and ecology of a few selected natural enemies, which are representative of the key species involved in different areas of the Cotton Belt. The species selected are: (a) *Geocoris punctipes* (Say) and the western bigeyed bug, *Geocoris pallens* (Stål); (b) the anthocorids, insidious flower bug, *Orius insidiosus* (Say) and minute pirate bug, *Orius tristicolor* (White); (c) the chrysopids, common green lacewing, *Chrysoperla carnea* Stephens and *Chrysoperla rufilabris* (Burmeister); (d) fire ants; (e) several species of spiders; (f) *Microplitis croceipes* (Cresson); (g) *Cardiochiles nigriceps* (Vierick); (h) *Trichogramma* spp.; and (i) tachinids, *Archytas marmoratus* (Townsend) and *Eucelatoria bryani* Sabrosky. Other species of predaceous and parasitic arthropods of cotton such as various species of coccinellids (lady beetles), other species of beetles, predaceous thrips and mites, various species of assassin bugs (family Reduviidae), damsel bugs (family Nabidae), and predaceous stink bugs (family Pentatomidae), as well as a number of other parasitic wasps in the families Ichneumonidae and Braconidae are also important depending on the geographical location and the specific phytophagous pest. Specific information on many of these species can be obtained from publications such as those by Quaintance and Brues (1905), Whitcomb and Bell (1964), van den Bosch and Hagen (1966), and Bohmfalk et al. (1983). Although it is beyond the scope of this chapter to discuss the biology and ecology of all these other beneficial arthropods, it should suffice to indicate that these too are important and should not be ignored when considering the natural enemy complex associated with cotton.

Three approaches are available for the utilization of natural enemies in pest management: importation of exotic natural enemies and augmentation and conservation of existing natural enemy populations. Our emphasis is on augmentation and conservation and the development of programs to actively manage the natural enemy complex (Price, 1981; Nordlund *et al.*, 1986; Vinson, 1988) similar to those developed for the pests. A primary aspect, discussed in Chapter 7 (this book) by Sterling *et al.*, is an improved understanding of the relationship between the densities of natural enemies and pests for the development of decision criteria. The other aspects emphasized here relate to environmental manipulations which maintain or increase the densities of the natural enemy complex or their suppressive effects on pest populations. This may involve provision of various environmental requisites, use of semiochemicals [chemi-

[1]All color plates can be found in the Appendix of this chapter.

cals involved in the interaction between organisms (Law and Regnier, 1971)], and modification of production or cropping practices.

Because of changes in approaches to cotton insect management brought about by the boll weevil eradication programs, the development of pyrethroid resistance in the tobacco budworm, increased pest status of the sweetpotato whitefly, *Bemisia tabaci* (Gennadius) and the cotton aphid, *Aphis gossypii* Glover, or changes needed as a result of recent sustainable agriculture initiatives, it is likely that renewed emphasis will be given to maximum utilization of the entire natural enemy complex (both predators and parasites) of all cotton pests. The primary emphasis in this chapter is on the factors that influence the abundance, phenology and efficacy of the selected species of natural enemies of cotton pests.

PREDATORS AND PARASITES AS NATURAL ENEMIES

Arthropod natural enemies in cotton fields are classified either as predators or parasites (van den Bosch and Hagen, 1966). Recognition of the distinction between the two groups is useful in understanding their biology, ecology and efficacy (Doutt, 1964).

A predator characteristically seizes or pierces its prey and either devours it or sucks it dry of its body fluids. An individual predator consumes a number of prey in completing its development. Both the adult and immature stages often feed on the same kind of prey. Generally, predators associated with cotton have a broad prey range. Predators either have chewing or piercing-sucking mouthparts and those with piercing-sucking mouthparts often inject powerful toxins and digestive enzymes that quickly immobilize the prey.

Parasites on the other hand, are insects that develop within or upon a single host and therefore are parasitic only in the immature stages. However, more than one parasite may develop in or on a single host. Adult parasites are generally free-living and feed on nectar, honeydew and sometimes host fluids. There are parasites that develop in all host life stages including the egg, larval or nymphal, pupal and adult. However, each species of parasite attacks only one life stage. Sometimes, parasite development extends over more than one life stage, such as egg-larval, larval-pupal, and nymphal-adult, but here again, one stage is attacked and development extends over two stages. The tendency is for the host range to be more limited than that of predators.

FACTORS INFLUENCING NATURAL ENEMY ABUNDANCE, PHENOLOGY AND EFFICACY

A review of the numerous factors influencing natural enemy abundance, phenology and efficacy is necessary for recognition of the opportunities for their maximum utilization. Some of these considerations relate to the intrinsic characteristics of each species and the interactions with the agroecosystem. These factors include: (a) habitat suitability; (b) availability of suitable prey or hosts; (c) insecticidal applications;

(d) geographical location; and (e) cotton varieties. The effects of some of these factors on entomophagous (feed on insects) arthropods have been discussed by Ables *et al.* (1983) and Goodenough *et al.* (1986). The system has numerous interactions and, because of the complexity, we have not been able to develop production systems that maximize the benefits from natural enemies. It is because of this complexity that recent research related to the development of decision-making technology, which incorporates the effects of natural enemies, has been on modeling (Sterling *et al.*, 1993; Wagner *et al.*, Chapter 6, this book; Sterling *et al.*, Chapter 7, this book). Computer models are needed that integrate the biology, ecology, and behavior of natural enemies with the objective of using this information to analyze and forecast the impact of the key natural enemies on the dynamics and economics of key pests.

HABITAT SUITABILITY

Because cotton is grown as an annual crop, it is available as a habitat for predators and parasites only during the growing season. In a single crop conventional production system, the noncrop period consists essentially of bare fields with minimal resources for supporting insect life. As the cotton plant grows and matures, changes occur that affect the availability of resources which are necessary for arthropod survival and reproduction. Such changes include alterations in the nutritional value of the cotton plant (Yokoyoma, 1978) and shifts in the makeup or abundance of host or prey popultions (Gonzalez and Wilson, 1982). Due to the ephemeral (transient) nature of the cotton ecosystem and the changes it undergoes during the growing season, colonization by arthropod predators and parasites is required. Sources of colonizer insects from the cultivated and uncultivated areas around cotton fields are of critical importance.

Fuchs and Harding (1976) determined that noncultivated habitats supported more predators than did cultivated habitats in the Lower Rio Grande Valley of Texas. They found the greatest numbers of predators in mixed grass habitats. Occurrence of vast cotton monocultures in some areas reduces the availability of colonizers. Intuitively, the number and kind of predators and parasites available to colonize cotton fields are determined by the surrounding area and its suitability for the development of natural enemy populations. The effectiveness of predators and parasites is dependent on their ability to move rapidly from the surrounding habitats into cotton fields. The timing of such movement is critical and thus the phenology (science concerned with the relationship of climate to biological phenomena) of the surroundings is important. Volatile chemicals (synomones) emanating from cotton plants are also important in the response of natural enemies to the cotton habitat (Vinson, 1988; Ridgway *et al.*, Chapter 11, this book).

Recognition of the importance of areas surrounding cotton fields as reservoirs of natural enemies (Fuchs and Harding, 1976; Gaylor and Gilliand, 1976; Pitre *et al.*, 1978; Roach, 1980) has led to studies of the movement of natural enemies into cotton. Lopez and Tectes (1976) documented the movement of predators from sorghum into cotton. In addition, means have been sought to exploit similar situations by strip cropping (Laster and Furr, 1972; Robinson *et al.*, 1972a, b; Schuster, 1980; DeLoach and Peters, 1972; Pair *et al.*, 1982).

Ehler and Miller (1978) concluded that key natural enemy species have adapted to habitats of low durational stability represented by the annual crop cotton habitat. These species then have become a key in the suppression of arthropod pest populations.

A mid-season decline of predators associated with cotton has been reported in different areas of the Cotton Belt (Dinkins *et al.*, 1970a, b; Schuster and Boling, 1974; Smith and Stadelbacher, 1978). Although various reasons have been cited as the cause, it is in part a function of plant maturity (Dean and Sterling, 1992). As the boll load increases, predator numbers decrease. The boll load measure reflects the completion of the period of blooming and a change in the availability of suitable food for both the pests and natural enemies.

AVAILABILITY OF SUITABLE PREY OR HOSTS

Another factor that influences predators and parasites is the availability of suitable prey or hosts, including the species, stage and number available during different periods of the cotton growing season. A key characteristic of predators and parasites relative to this factor is the host range. A natural enemy with a broad host range would have a greater chance of effective colonization. However, from a grower viewpoint, a broad prey or host range may be detrimental because it reduces the regulatory effects on specific pest species. Differences in the host or prey range of predators and parasites would certainly have an influence on the population dynamics of the two types of natural enemies. Thus, preference and specificity of the natural enemies are important considerations. Ables *et al.* (1978) demonstrated this effect for several predator species with different densities of the cotton aphid and tobacco budworm eggs as prey.

Chemicals [kairomones—substance(s) produced or acquired by an organism that, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioral or physiological reaction that is adaptively favorable to the receiver but not to the emitter (Brown *et al.*, 1970)] associated with specific pest species also influence the host or prey finding and selection behavior of natural enemies (Vinson, 1988). See Chapter 11, this book, for a discussion of behavior-mediating chemicals.

A primary concern relative to natural enemy abundance and efficacy are the functional and numerical responses (Solomon, 1949) of the predators or parasites to host or prey density. The functional response refers to changes in the number of prey consumed or hosts parasitized per unit time in relation to the change in prey density. The numerical response refers to the increase in numbers of predators or parasites in response to increases in prey or host density. From the standpoint of the short term effects of natural enemies on pest densities, the functional response is important. However, in relation to colonization of the cotton habitat, the numerical response is important.

The suitability of the host or prey for development of the predator or parasite is also important. A high level of suitability should result in higher rates of development, survival and fecundity which all contribute to an increase in the number of natural enemies in response to an increase in prey or host density.

Some natural enemies feed on plant juices, nectar or pollen. This feeding is important to the survival of the species during periods when prey or host abundance is limited. It may also be important in earlier colonization and persistent occurrence in the cotton habitat.

INSECTICIDAL APPLICATIONS

One of the most important factors influencing natural enemy presence and abundance in cotton is application of insecticides; a major area of the conservation approach to biological control. The adverse effects of insecticides on beneficial arthropods are affected by the rate, time, frequency and method of application (Ables *et al.*, 1983). Other factors are: (a) the acute toxicity and persistence of the insecticides used (Plapp and Vinson, 1977; Plapp and Bull, 1980; Chang and Plapp, 1983; Bull *et al.*, 1989; Pree *et al.*, 1989); (b) size of the area treated; and (c) the diversity of the agroecosystem (Bradley *et al.*, 1987). These adverse effects on natural enemies in cotton and subsequent effects on pest populations by the direct application of insecticides to the field have been amply reviewed especially in relation to the bollworm/tobacco budworm (Bradley *et al.*, 1987). Insecticide use in surrounding areas also influences populations in cotton fields because of drift and the effects on potential colonizers. Repetitive use of insecticides both in cotton and the surrounding areas may be an important factor in determining natural abundance of predators and parasites. Shifts in the pattern of use of insecticides also may have an impact on the species composition of the natural enemy complex.

A major concern, as we attempt to manage resistance of the tobacco budworm to the pyrethroids, is the effect of resistance management strategies on natural enemies. Use of different classes of insecticides or mixtures during different periods in the growing season would likely have a major impact on the composition and abundance of the natural enemy complex. In addition, the need to treat eggs and very small larvae to obtain satisfactory control of resistant insects (because of the greater susceptibility of the early instar larvae) limits the potential for maximum utilization of predators and parasites.

GEOGRAPHICAL LOCATION

Considerable variability has been identified in the natural enemy complexes of different areas of the Cotton Belt (Ables *et al.*, 1983). These differences reflect variability in climate and local cultural practices which include tillage systems, chemical weed control, irrigation, planting dates and densities, cultivars (varieties) used, row spacing, crop rotation, fertilization, planting design and management of non-crop plants. The interaction of these factors provide a characteristic natural enemy complex at each location. Our understanding of the reasons for the differences will improve our ability to utilize predators and parasites in pest management programs.

Mode of overwintering and the suitability of habitats available for overwintering are related to geographical location and cultural practices but have not received sufficient attention by researchers. In most areas of the Cotton Belt, harsh winter conditions and

scarcity of suitable prey or hosts are major factors in reducing the numbers of natural enemies available for colonization in the spring. It is especially important to understand the overwintering dynamics of pest and natural enemy populations to be able to produce multi-year models as an extension to current seasonal models such as TEXCIM for Windows (Sterling *et al.*, 1993). Although forecasting models are currently available for some key pests of cotton, they are in a more elementary state for natural enemies. Until these models become available, counts of natural enemies in cotton fields can be entered into models to forecast their short-term impact using the TEXCIM approach.

COTTON VARIETIES

Populations of natural enemies also are affected by cotton varieties (Ables *et al.*, 1983; Treacy *et al.*, 1985), especially varieties with host plant resistance characters. These varieties may limit the number of prey or hosts available as well as the habitat quality afforded by the plant. Shepard *et al.* (1972) reported that hirsute (hairy) genotypes generally supported fewer natural enemies than did early maturing glabrous (smooth) genotypes. Mussett *et al.* (1979) reported that, when compared to a standard commercial variety, predator populations were reduced by up to 68 percent in cotton lines bred for bollworm/tobacco budworm resistance. Numerous studies comparing the effect of the nectariless and the nectaried characters on the natural enemy complex have generally concluded that the nectariless character is detrimental to the abundance or effectiveness of the natural enemy complex (Schuster *et al.*, 1976; Calderon, 1977; Henneberry *et al.*, 1977; Lingren and Lukefahr, 1977; Mussett *et al.*, 1979; Agnew *et al.*, 1982; DeLima and Leigh, 1984; Thead *et al.*, 1985; Treacy *et al.*, 1987a).

One important component of future pest management programs may lie in habitat manipulation both inside and outside the cultivated field (Whitcomb, 1974). Whitcomb stated that population manipulation systems should be based on a thorough understanding of the agroecosystem. The predators and parasites that play a role in checking the abundance of pests, their life histories, and factors affecting their populations must be known. He further stated that the source of beneficial insects and the cause of population fluctuations is almost a separate discipline of science in itself.

PREDATORS

The most immediate opportunities for substantial use of entomophages are related to increased use of predators for management of bollworm/tobacco budworm (Ables *et al.*, 1983). More recent research has identified other predators that are important in the suppression of boll weevil and cotton fleahopper populations that should be considered. Several important species of insect and spider predators have been selected for discussion here. These include two species each of bigeyed bugs, chrysopids and anthocorid bugs. Fire ants are discussed as a group with primary emphasis on the red imported fire ant, *Solenopsis invicta* Buren. The other predators discussed are spiders; these are also discussed as a group.

INSECTS

Bigeyed Bugs—The subfamily Geocorinae of the family Lygaeidae, is of interest because unlike most members of this family which are seed feeders, all known species are predaceous (Readio and Sweet, 1982). The species are not obligatory predators in that they feed on seeds (Sweet, 1960), plant juices (Ridgway and Jones, 1968; Stoner, 1970) and cotton extrafloral nectar (Yokoyama, 1978).

These predators are commonly called bigeyed bugs because of the large conspicuous eyes on their distinctively broad heads (Plate 3-2). The compound eyes protrude laterally beyond the pronotum (the shield-like structure on top of the first thoracic segment just behind the insect's head). Although several *Geocoris* species are associated with cotton, *Geocoris punctipes* and the western bigeyed bug, *Geocoris pallens*, apparently are the most important species.

Geocoris punctipes is widely distributed throughout much of the southern two-thirds of the United States and its range extends southward into Colombia, South America (Readio and Sweet, 1982). The western bigeyed bug has been collected from most of the western states and its range extends eastward to Indiana, Illinois, Missouri and Arkansas (Readio and Sweet, 1982). Numerous studies on the occurrence of the two species in the Cotton Belt indicate that *Geocoris punctipes* is less abundant than the western bigeyed bug in California (van den Bosch and Hagen, 1966), but it becomes predominant in eastern areas of the Cotton Belt (Butler 1966a; Roach, 1980; Parencia *et al.*, 1980; Schuster and Boling, 1974; Pitre *et al.*, 1978; Dinkins *et al.*, 1970a, b; Roach, 1980; Crocker and Whitcomb, 1980).

Development in both species is hemimetabolous (incomplete metamorphosis) in that they go through the egg, nymphal, and adult stages (Champlain and Sholdt 1966; Tamaki and Weeks, 1972). There are five nymphal instars. Davis (1981) described the eggs as ovoid with one end tapering more than the other. Chorionic processes located at the blunt end of the egg form a ring of five to seven hooked, peg-like structures below which conspicuous red eye spots appear about five days before eclosion. The length and width of eggs average 0.038 inch (0.97 millimeter) by 0.015 inch (0.37 millimeter) and 0.035 inch (0.88 millimeter) by 0.015 inch (0.37 millimeter) for *Geocoris punctipes* and western bigeyed bug, respectively. The nymphs are pale gray to greenish gray in color with the abdomen either mottled or streaked with red (Plate 3-3). Second through fifth instars of *Geocoris punctipes* have the head with a dark sulcus (groove) extending from the tylus (a central prominence on the upper side of the head) onto the vertex of the head and the abdomen with broken red streaks running laterally across segments while western bigeyed bugs have the head with a faint sulcus extending from the tylus onto the vertex and the abdomen with red mottling interspersed over the entire surface. The females of western bigeyed bugs and *Geocoris punctipes* average about 1/6th inch (4.07 millimeters) and 3/16ths inch (4.45 millimeters) in length, respectively, while the males average about 5/32nds inch (3.64 millimeters) and about 1/6th inch (4.07 millimeters), respectively. In *Geocoris punctipes* adults, the head is smooth, shiny; the sulcus extends from tylus onto the vertex; the bucculae (ridge

beneath the head on either side of the proboscis or mouth of some insects) does not meet directly behind the labium (lower lip) but forms a narrow v-ridge which runs to the posterior margin of the head. Western bigeyed bug adults have a granulose head; sulcus not extending beyond the tylus; the bucculae meeting directly behind the labium; scutellum (the area of the wing-bearing plate of the top of the second or third thoracic segments that is posterior to the V-shaped notal ridge) distinctly longer than wide; head with various light markings, particularly a yellow comma-shaped area on the outer lateral edge of each ocellus (single simple eye), black pronotal calluses (thickened or cuticular swellings on the body of an insect) generally have a light oval spot in the center of each callus; posterior half of pronotum is generally white; scutellum evenly convex with a smooth ridge down entire midline of scutellum; corium (the middle part of the basally thickened front wings of insects) of wing yellowish-white and punctuation on wing distinct.

There have been numerous studies on the effect of temperature and diet on the development of *Geocoris punctipes* and western bigeyed bug (Champlain and Sholdt, 1966, 1967a, b; Butler, 1966b; Dunbar and Bacon, 1972a, b; Tamaki and Weeks, 1972; Crocker *et al.*, 1975; Davis, 1981; Cohen and Debolt, 1983). Rate of development is influenced primarily by temperature and food quality. Although feeding on seeds, plant juices and nectar does occur, prey are necessary for both species to complete their life cycles and to reproduce. Green beans have been used as a source of moisture in most studies, but Cohen and Debolt (1983) showed that water was just as good for rearing. Considerable variation in the rate of development has been observed, probably due to differences in the food and rearing conditions. Dunbar and Bacon (1972a) and Davis (1981) evaluated rates of development of eggs and nymphs for both *Geocoris punctipes* and western bigeyed bug using similar temperature regimes and the same kind of food (Table 1). The data for selected temperatures demonstrate the number of days required and the better adaptation of the western bigeyed bug to higher temperatures. This may contribute to its predominance in the hotter southwestern areas of the Cotton Belt.

Mating may occur on the day of adult emergence and the preoviposition (pre-egglaying) period at 79F (26.1C) for both species is about five days. The adults are relatively long-lived (two or three months), at least in the laboratory. Total fecundity per female at the optimum temperature was a mean of 301 eggs at 90F (32.2C) and 416 at 84.9F (29.4C) for the western bigeyed bug and *Geocoris punctipes*, respectively (Davis, 1981). During periods of peak oviposition, females oviposited between five and ten eggs per day.

Both *Geocoris punctipes* and western bigeyed bug overwinter as adults on winter crops (Whitcomb and Bell, 1964); they may take cover in ground trash during cooler periods (Tamaki and Weeks, 1972). Adult movement into cotton appears to be related to the fruiting cycle (Dean and Sterling, 1992). Studies indicate that the seasonal occurrence of *Geocoris punctipes* and western bigeyed bug is related to blooming of cotton. A late season decline in the numbers of *Geocoris* spp. has been observed in most areas of the Cotton Belt (Fuchs and Harding, 1976; Pitre *et al.*, 1978; Roach, 1980; Smith and Stadelbacher, 1978; Dinkins *et al.*, 1970a, b), which has been attrib-

Table 1. Effects of selected temperatures on development of *Geocoris punctipes* and western bigeyed bugs, *Geocoris pallens* as reported from two separate studies.

Average number of days (percent survival) to complete stage					
		Study no. one[1]		Study no. two[2]	
Life Stage	Temperature F (C)	*Geocoris punctipes*	*Geocoris pallens*	*Geocoris punctipes*	*Geocoris pallens*
Egg	75 (23.9)	18.7 (85.7)	16.3 (81.3)	14.4 (82.2)	12.3 (80.3)
	80 (26.7)	10.5 (83.2)	8.9 (95.9)	8.7 (76.7)	7.1 (86.6)
	95 (35.0)	6.4 (74.7)	4.9 (93.9)	5.7 (65.7)	4.1 (83.0)
	99 (37.8)	6.5 (11.0)	4.2 (85.7)	0.0	0.0
Nymph	75 (23.9)	41.4 (71.4)	49.0 (1.0)	37.3 (71.2)	42.2 (35.3)
	80 (26.7)	27.6 (56.8)	27.3 (28.6)	25.3 (63.6)	24.1 (50.4)
	95 (35.0)	16.6 (48.5)	13.6 (50.5)	17.0 (8.9)	12.1 (60.0)
	99 (37.8)	0.0 (0.0)	12.3 (24.5)	0.0	0.0

[1]Data from Davis, L. D., Jr. 1981.
[2]Data from Dunbar, D. M. and O. G. Bacon. 1972a.

uted to late season insecticide applications (Dinkins *et al.*, 1970b) and a natural decline in numbers late in the season (Smith and Stadelbacher, 1978). Yokoyama (1978) suggested that the decreasing availability of extrafloral nectar is an important factor in this decline. The distribution of the different stages of *Geocoris* on the cotton plant during the season has also been attributed to the effect of extrafloral nectaries. Eggs have been found on the underside of cotton leaves close to extrafloral nectaries. The nymphs and adults have also been observed to be more common on the lower parts of plants where they are apparently associated with the extrafloral nectaries (Cosper *et al.*, 1983). The higher numbers of *Geocoris* spp. observed on nectaried as compared to nectariless cotton genotypes (Schuster *et al.*, 1976; Henneberry *et al.*, 1977) supports the conclusion that extrafloral nectar is important in the development of *Geocoris* spp. populations in cotton. Gonzalez *et al.* (1977) also suggested that the build-up of prey, especially minor pests of cotton, which is influenced by the fruiting cycle, may also contribute to the seasonal pattern of *Geocoris* abundance.

Geocoris punctipes and western bigeyed bug have piercing-sucking mouthparts; they attack by waiting or running up to the prey, extending the beak and quickly inserting the stylets (Crocker and Whitcomb, 1980). Both species have a relatively broad prey range (Stoner, 1970; Tamaki and Weeks, 1972; Crocker and Whitcomb, 1980). Important prey relative to cotton are spider mites, cotton fleahoppers, whiteflies, aphids, plant bugs, thrips and lepidopterous eggs and larvae. Among the lepidopterous eggs and larvae are the bollworm and tobacco budworm (Lingren *et al.*, 1968; Lopez *et al.*, 1976; McDaniel and Sterling, 1982; Bell and Whitcomb, 1964; van den Bosch *et al.*, 1969), pink bollworm, *Pectinophora gossypiella* (Saunders), (Orphanides *et al.*, 1971; Henneberry and Clayton, 1985), cabbage looper, *Trichoplusia ni* (Hübner),

(Ehler *et al.*, 1973), and cotton leafworm, *Alabama argillacea* (Hübner), (Gravena and Sterling, 1983). Field and laboratory studies have shown *Geocoris* spp. to be particularly effective predators of lepidopterous eggs and early instar larvae (Eveleens *et al.*, 1973; Bell and Whitcomb, 1964; Ehler *et al.*, 1973; Lopez *et al.*, 1976; Lawrence and Watson, 1979; Chiravathanapong and Pitre, 1980). *Geocoris punctipes* also is a key predator of the cotton fleahopper (Breene *et al.*, 1989b).

An aggregation response by *Geocoris punctipes* adults to selected dosages of aqueous homogenates of terminal instar bollworm and fall armyworm, *Spodoptera frugiperda* (J. E. Smith), larvae applied to whorl stage corn has been observed apparently in response to chemical stimuli (kairomones) (Gross *et al.*, 1985).

Chrysopids—Chrysopids are important predators and two species, *Chrysoperla carnea* (common green lacewing) and *Chrysoperla rufilabris*, are frequently associated with cotton. Green lacewing larvae are commonly called aphidlions. They prey on a wide variety of small soft-bodied insects and mites (Ridgway and Kinzer, 1974). Of particular importance relative to cotton, is their ability to prey on aphids, thrips, whiteflies, mites and eggs and small larvae of several species of lepidopterous pests.

The two species differ significantly in their geographical distribution. Where they occur together, their relative and seasonal abundance often differ (Tauber and Tauber, 1983). The common green lacewing is widely distributed within North America and has been collected in Alaska, every Canadian province, every state in the contiguous United States and as far south as the Federal District in Mexico. The distribution of *Chrysoperla rufilabris* is more restricted and is limited to eastern and midwestern parts of North America, extending from eastern Canada through Florida and northeastern Mexico (Tauber and Tauber, 1983). Its range overlaps with that of common green lacewing from eastern Canada to northeastern Mexico, but in the southeastern United States and Mexico, *Chrysoperla rufilabris* is generally more common. This difference in distribution is attributed to the differential response of the two species to humidity (Tauber and Tauber, 1983). Under high humidity conditions common in the southeastern United States, the developmental potential of *Chrysoperla rufilabris* is slightly higher than the common green lacewing. Low humidity substantially reduces the developmental and reproductive potentials of *Chrysoperla rufilabris*, but has no negative effects on common green lacewing. Thus, the common lacewing is favored in the less humid southwestern parts of the United States.

These generalizations on the distribution of the two species are borne out by research conducted in different parts of the Cotton Belt. In California, the common green lacewing is mentioned as the primary species occurring on cotton (van den Bosch and Hagen, 1966; Ehler *et al.*, 1973; Gonzalez *et al.*, 1977; Wilson and Gutierrez, 1980). In the central and southeastern parts of the Cotton Belt, both species occur together, but there are seasonal differences. During the early season, common green lacewing has been found to predominate, but during mid- to late-season, *Chrysoperla rufilabris* was the most abundant (Burke and Martin, 1956; Bell and Whitcomb, 1964; Dinkins, 1970a, b; Agnew et al., 1981). In these areas, it appears that

Chrysoperla rufilabris is more important relative to the impact on bollworm/tobacco budworm and other pests in cotton.

The adults are about 1/2 to 3/4ths inch (12.5 to 19.1 millimeters) long and are yellowish-green with golden eyes and large, delicate, netted wings (Plate 3-4). *Chrysoperla* adults are identified by criteria provided by Bickley and MacLeod (1956) and photos and keys of Agnew *et al.* (1981). According to Bram and Bickley (1963), both species have the antennae, except for the second segment, entirely pale or with the basal fourth pale, apical third may be brownish, but not dark brown and the antennae are unmarked (no black or brown ring on the second segment). Adults with the above characteristics and with all veins entirely pale, or at most with only an occasional dark crossvein, and with a definite narrow black or dark-red band from eye to mouth over the genae; varying amounts of red suffusion adjacent to the black band; and hind wing bluntly rounded at apex are common green lacewings (Plate 3-5). Adults of *Chrysoperla rufilabris* have the gradates and some other veins marked with black or brown; pronotum, thorax and abdomen without orange spots; and a red stripe on genae from eye to mouth. According to Agnew *et al.* (1981), separation of *Chrysoperla rufilabris* is by: (a) gradate veins dark colored, (b) pronotum and abdomen without dark orange markings, and (c) genae with red markings running from eye to mouth. The common green lacewing has all veins pale with only an occasional dark crossvein and the genae with a straight dark line, often suffused with red, running from eye to mouth.

The stage most likely to be found in cotton fields is the larval stage. In both species, there are three larval instars. The larvae are naked (not trash carriers), campodeiform (body elongate and somewhat flattened, thoracic legs well developed, and the larvae are usually active), the abdomen is not humped and with long and slender jaws (Tauber, 1974). The most striking specialization of the larvae is the prolongation of the maxillae and the mandibles to form sickle shaped sucking tubes that are efficiently used in catching and feeding on prey (Smith, 1922). Tauber (1974) provided characteristics by which different instars of the two species can be separated. Relatively distinct differences are evident between the larvae of the two species especially in the later instars (Plates 3-6 and 3-7).

Development in the common green lacewing and *Chrysoperla rufilabris* is holometabolous (complete metamorphosis) involving four distinct developmental stages: egg, larva, pupa and adult. Both species lay eggs singly. The eggs are attached at the extreme posterior end to a hyaline, hardened gelatinous stalk that is from about 1/6th to 1/3rd inch (4 to 8 mm) long (Smith, 1922) (Plate 3-8). The egg is elongate-elliptical in shape and green to yellowish in color. As the embryo develops, the egg becomes gray with darker areas. The larvae, which are extremely cannibalistic, undergo three molts, the last molt taking place inside the cocoon constructed by the third-instar larva. The cocoon is pure white in color and is spherical or slightly elongated in shape (Plate 3-9). The cocoons are found in areas of the plant where plant parts form an irregular cavity and inside the bracts (between the bracts of squares or bolls) of cotton fruit. The pupae are exarate with freely movable legs and emerge from the cocoon by biting a round lid in the cocoon. The molt to the adult occurs after emergence.

Development of common green lacewing and *Chrysoperla rufilabris* under different rearing conditions and different larval food are summarized in Table 2. Of major concern relative to the direct effects of common green lacewing and *Chrysoperla rufilabris* on cotton pests is the length of the larval stage which is predatory and the ability to develop on a wide range of prey.

Table 2. Developmental time of the stages of common green lacewing, *Chrysoperla carnea*, and *Chrysoperla rufilabris* affected by temperature and food source.

Temperature F (C)	Food source	Average developmental time (Days) Egg	Larva	Pupa		Source/ reference
		Chrysoperla carnea				
75 ± 7.2 (24 ± 4)		5.3	18.3	9.6		Toschi (1965)
Avg. min. of 75F to Avg. max. of 88F	aphids	4.9	13.7	8.1		Burke & Martin (1956)
				male	female	
59 (15)	Angoumois grain moth eggs	13.1	28.8			Butler & Ritchie (1970)
68 (20)		6.3	13.9	13.3	13.8	
77 (25)		4.2	10.6	8.8	8.8	
86 (30)		3.1	7.1	6.6	6.9	
90 (32.2)			6.5	6.1	6.2	
90 (35)			6.6	5.9	6.2	
77 ± 2.7 (25 ± 1.5)	bollworm/tobacco budworm eggs		8.6			Boyd (1970)
	bollworm/tobacco budworm larvae		11.4			
	cotton aphids		8.8			
	carmine spider mites		16.0			
	Angoumois grain moth eggs		8.2			Tauber & Tauber (1983)
72 (22.2) (35%RH')	Angoumois grain moth eggs		25.5			
72 (22.2) (55%RH)			25.9			
72 (22.2) (75%RH)			25.2			
		Chrysoperla rufilabris				
Avg. min. of 75F to avg. max. of 88F	aphids	3.7	10.4	6.5		Burke & Martin (1956)
72 (22.2) (35%RH)	Angoumois grain moth eggs		28.4			Tauber & Tauber (1983)
72 (22.2) (55%RH)			26.4			
72 (22.2) (75%RH)			24.2			
81 ± 3.6 (27 ± 2) (70%RH)	Angoumois grain moth eggs		21.6			Elkarmi *et al.* (1987)
80 (26.5) (80%RH)	cabbage looper eggs	5.7	15-17.75			Ru *et al.* (1976)
72.5 (22.5)	cowpea aphid		23.3			Hydorn (1971)

Table 2. Continued

Temperature F (C)	Food Source	Average developmental time (Days) Egg	Larva	Pupa	Source/ reference
	green peach aphid		22.0		
	citrus white fly		26.8		
	green lynx spider		28.5		
	greater wax moth		24.2		
	red flour beetle		27.3		
	vinegar fly		26.8		
79 (26)	bollworm		21.7		Hydorn (1971)
	potato tuberworm		19.4		

[1]RH refers to relative humidity.

For the common green lacewing, Burke and Martin (1956) reported a preovipostion period of 13 days with an oviposition period of 20.6 days and a fecundity of 32 eggs per female. According to Hydorn (1971), this was the first record of moderately high fecundity and long longevity of captive adults. The adults were fed a mixture of honey, water and an artificial nutrient powder. Other research (Tauber and Tauber, 1983) conducted at 71.8F (22.1C) and relative humidities of 35, 55 and 75 percent showed a preoviposition period ranging from 5.3 to 7.4 days, a total fecundity, over a 30-day period, of 273 to 328 eggs per female, and a mean number of eggs per female over a 3-day period of 27 to 33 eggs. The adult food was a 1:1:1:1 mixture of Wheast®, protein hydrolysate of yeast, sugar and water. Elkarmi *et al.* (1987) reported a fecundity of 13.3 eggs per female per day over a 30-day period for the common green lacewing at 80.6F (27C) and 75 percent relative humidity. For *Chrysoperla rufilabris*, Burke and Martin (1956) reported that mating occurred within the first two days of adult activity, a preoviposition period of 8.2 days, an oviposition period of 11.3 days and a total fecundity of 31.2 eggs per female. At 72F (22.2C) and at 35, 55, and 75 percent relative humidity, Tauber and Tauber (1983) reported that the preoviposition period for *Chrysoperla rufilabris* ranged from 5.8 to 12.4 days, total fecundity over a 30-day period ranged from 87 to 280 eggs per female and a mean oviposition rate per female over a 3-day period ranging from 8.8 to 28.3 eggs. Elkarmi *et al.* (1987) reported an optimum fecundity at 80.6F (27C) and 70 percent relative humidity of 25.2 eggs per female per day over a 30-day period and a three-day preoviposition period for *Chrysoperla rufilabris*. Hydorn (1971) found that average longevity for *Chrysoperla rufilabris* was over 30 days on a number of larval diets, but longevity was reduced when larvae were reared on vinegar flies, *Drosophila melanogaster* Meigen, and red flower beetles, *Tribolium castaneum* (Herbst), and the average number of eggs per female ranged from 29 to 208 with an average number of eggs per female per day of 1.6 to 9.

Overwintering is another important aspect of the development of the common green lacewing and *Chrysoperla rufilabris* relative to biology and ecology. Both species overwinter in diapause (New, 1975) which is induced by the short photoperiods occur-

ring at the end of summer. Both sexes of common green lacewing undergo a change in color when in adult diapause and become brownish-yellow with rusty red spots on the dorsum (upper side). Although the mode of overwintering of *Chrysoperla rufilabris* has not been studied as extensively as that of the common green lacewing, Putman (1937) reported that *Chrysoperla rufilabris* overwinters in diapause in the prepupal stage in the cocoon; however, Burke and Martin (1956) reported that this species overwinters as an adult in Central Texas.

The adults of the common green lacewing and *Chrysoperla rufilabris* are not predatory and they primarily feed on honeydew, pollen and sweet plant exudates. The common green lacewing has been studied more extensively. The adult response of the common green lacewing toward honeydew has led to research on the use of artificial honeydew to attract adults to field crops and to increase oviposition (Hagen *et al.*, 1971; Hagen and Hale, 1974). Artificial honeydew, containing enzymatic protein hydrolysates of Brewer's yeast or Wheast®, (Hagen and Tassan, 1970), has an attractive ingredient, which is a breakdown product of the amino acid tryptophan (Hagen *et al.*, 1976; van Emden and Hagen, 1976). The affinity of the common green lacewing for cotton was demonstrated in the response during early season of adults to traps baited with caryophyllene, a sesquiterpene hydrocarbon that is a major component of the aroma of a cotton field (Flint *et al.*, 1979).

Jones *et al.* (1977) reported that from 9 a.m. to 6 p.m., the adult common green lacewings are inactive and found primarily in shady areas on the undersides of leaves. This makes them difficult to see during the day. Feeding occurs mostly between 6 to 10 p.m. and between 2 to 9 a.m., peaking between 7 and 8 a.m. Mating occurs primarily between 7 p.m. to 2 a.m. with a peak between 8 to 10 p.m. Males mate when three to four days old and remate readily after a two- to four-day resting period. Most females mate at four days of age and few remate during a 30-day period. Oviposition usually occurs between 8 p.m. to 1 a.m. with a major peak between 9 to 10 p.m.

Adult dispersal behavior is important relative to the colonization of cotton by the common green lacewing. Duelli (1980a, b) reported that adult emergence occurs at night with a prominent peak during the first hour of the scotophase (dark phase). Takeoff is elicited by a decrease in light intensity and occurs shortly after sunset. These adaptive dispersal flights during the first two to three nights of adult life are straight downwind for an average distance of 26 miles (40 kilometers) per night and at an average height of 19.7 to 39.4 feet (6 to 12 meters). During these flights, there is no response to honeydew, thus the flights are referred to as obligatory migration flights. After two to three days, honeydew provides a strong landing stimulus and the flights which are now at a height lower than 9.8 feet (3 meters), are appetitive. Honeydew is located by upwind flight that rarely exceeds 3.3 feet (1 meter) above crop level.

Understanding the predatory capabilities of the larval stage is important in assessing the impact of common green lacewing and *Chrysoperla rufilabris* as predators in cotton. The primary research emphasis has been on the common green lacewing and the interaction with lepidopterous cotton pests. The larvae are efficient predators of eggs and early instars of the bollworm and tobacco budworm (Fletcher and Thomas,

1943; Lingren *et al*., 1968; van den Bosch *et al*., 1969; Lopez *et al*., 1976). McDaniel and Sterling (1982) and McDaniel *et al*., (1981) verified predation of radioactive tobacco budworm eggs and larvae by *Chrysoperla* spp. larvae in cotton fields. Larvae of the common green lacewing are also important predators of eggs and young larvae of pink bollworm (Orphanides *et al*., 1971; Henneberry and Clayton, 1985), cabbage looper (Ehler *et al*., 1973), and beet armyworm, *Spodoptera exigua* (Hübner), (Eveleens *et al*., 1973). Butler and Henneberry (1988) determined that larvae consumed all stages of the sweetpotato whitefly in the laboratory.

Boyd (1970) reported the following predatory capabilities of common green lacewing on cotton: (a) prey preference in descending order was 1st instar bollworm/tobacco budworm larvae > cotton aphids > bollworm/tobacco budworm eggs > carmine spider mites, *Tetranychus cinnabarinus* (Boisduval); (b) all larval instars preyed on bollworm/tobacco budworm eggs, but were able to capture or kill only small to medium sized bollworm/tobacco budworm larvae; (c) larvae spent about 50 percent of their time in search of prey; and (d) larvae were found primarily on the top half of cotton plants (77 percent) and inside the bracts of squares (41 percent). Stark and Whitford (1987) reported a mean search rate of 2.69×10^{-5} acres (1.08×10^{-5} hectare) per predator per day or 0.36 row-feet (0.11 row-meter) per predator per day for third instar common green lacewing larvae feeding on different densities of tobacco budworm eggs on caged cotton. The importance of prey preference of the larvae was established by Ables *et al*. (1978) who reported that larvae preyed on significantly fewer bollworm/tobacco budworm eggs when cotton aphids were present as alternate prey.

There is evidence that a kairomone(s) associated with bollworm oviposition affects the prey-finding behavior or acceptance of eggs by common green lacewing larvae and moth scales also have kairomonal properties (Lewis *et al*., 1977; Nordlund *et al*., 1977).

Effects of insecticides and host plant resistance characters on common green lacewing and *Chrysoperla rufilabris* are important. Populations of common green lacewing showing tolerance to pyrethroids appear to be fairly common (Plapp and Bull, 1978; Shour and Crowder, 1980; Ishaaya and Casida, 1981; Grafton-Cardwell and Hoy, 1985; Pree *et al*., 1989) and resistance to some types of organophosphorus and carbamate insecticides has been reported (Lingren and Ridgway, 1967; Plapp and Bull, 1978; Grafton-Cardwell and Hoy, 1985, 1986; Pree *et al*., 1989). Two host plant resistance characters in cotton affect *Chrysoperla* spp. Treacy *et al*. (1987a) showed that fewer bollworm eggs were destroyed by *Chrysoperla rufilabris* larvae on a pilose (soft hairy) cotton than on a hirsute (coarse hairy) cotton and egg predation was greater on smoothleaf cotton than on hirsute cotton. Cotton leaf trichomes (epidermal hairy structures) inhibited movement of the *Chrysoperla rufilabris* larvae on the leaf surfaces, and reduced predation by *Chrysoperla rufilabris*. The effect of the trichomes was reduced for third instar larvae. Elsey (1974) showed that the first and second instars of common green lacewing are able to search much faster on cotton than on tobacco because of the decreased density of glandular trichomes in cotton. The nectariless character significantly reduced densities of common green lacewing more so than *Chrysoperla rufilabris* (Schuster *et al*., 1976). Boyd (1970) suggested that during

periods of low prey availability on cotton, larvae of common green lacewing could supplement their diet with cotton plant nectar. Calderon (1977) found that common green lacewing larvae and adults preferred to feed on aphids and aphid honeydew, rather than on cotton nectar; however, female longevity and fecundity (egg-laying or reproductive ability) were both reduced on nectariless cotton.

Anthocorid Bugs—Two anthocorids are important predators of cotton pests: the insidious flower bug, *Orius insidiosus* and the minute pirate bug, *Orius tristicolor*. The insidious flower bug is more common in the eastern United States while minute pirate bug is primarily a western species; however, their distributions do overlap (Herring, 1966). Studies conducted in cotton throughout the Cotton Belt indicate the predominance of minute pirate bug in the southwest and of insidious flower bug in the South and Southeast. The insidious flower bug has been reported to be a common predator in cotton fields in: South Carolina (Roach, 1980; Roach and Hopkins, 1981); Mississippi (Smith *et al*., 1976a,b; Smith and Stadebacher, 1978; Pitre *et al*., 1978; Schuster *et al*., 1976; Dinkins *et al*., 1970a, b; Parencia *et al*., 1980; Schuster, 1980); Louisiana (Watve and Clower, 1976); southeastern Missouri (DeLoach and Peters, 1972); Arkansas (Whitcomb and Bell, 1964; Bell and Whitcomb, 1964); and Texas (Quaintance and Brues, 1905; Ewing and Ivy, 1943; Fletcher and Thomas, 1943; Ridgway and Lingren, 1972; Shepard and Sterling, 1972b; Schuster and Boling, 1974; Lingren and Ridgway, 1967; McDaniel *et al*., 1981; McDaniel and Sterling, 1982). In contrast, minute pirate bug has been reported to be the most common *Orius* species in: California (van den Bosch and Hagen, 1966; Ehler *et al*., 1973; Eveleens *et al*., 1973; Gonzalez *et al*., 1977; Stoltz and Stern, 1978; Yokoyama, 1978; Byerly *et al*., 1978; Wilson and Gutierrez, 1980); Arizona (Wene and Sheets, 1962; Butler, 1966a); western counties of Arkansas (Whitcomb and Bell, 1964); the western part of the Lower Rio Grande Valley (Schuster and Boling, 1974); and West Texas (Bohmfalk *et al*., 1983).

The anthocorids differ from the other members of the Order Heteroptera (true bugs) in that they have a definite embolium (a narrow strip of the corium) of the forewing (Deitz *et al*., 1976). Both the insidious flower bug and minute pirate bug are black and white and measure less than 1/8th inch in length (1.6 to 2.2 millimeters) (van den Bosch and Hagen, 1966; Isenhour and Yeargan, 1981) (Plate 3-10). Both sexes are similar in appearance, but the males are slightly smaller. Both species are somewhat flattened, and ovoid (egg-shaped) and they have a prominent beak for piercing soft bodied prey and sucking body fluids. The clavus and corium are morphological structures important in separating the two species. According to Kelton (1963), the antennae, legs and the hemelytra of both species are partly black. The clavus is the oblong or triangular anal portion of the front wing and the corium is the elongate, usually thickened, basal portion of the front wing. The clavus is mostly pale as is the corium in insidious flower bugs while in minute pirate bugs, the clavus is mostly black. When the clavi (plural for clavus) of insidious flower bug are dark, males can be separated from minute pirate bugs by the structure of the left claspers (modified structures that assist the males in mating). The females have the lateral margins of the pronotum

much more rounded with the calluses flat and poorly delimited (Herring, 1966). The conspicuously bicolored hemelytra with dark clavi will usually separate the minute pirate bug from the insidious flower bug. In the minute pirate bug females, the lateral margins of the pronotum are much straighter and the calluses are much more clearly delimited and elevated than in the insidious flower bug (Herring, 1966).

Development in both species is hemimetabolous involving three stages: egg, five nymphal instars and adult. The inconspicuous eggs are oviposited in soft plant tissue at an angle almost perpendicular to the surface, leaving the concave egg caps showing above the surface (van den Bosch and Hagen, 1966; Isenhour and Yeargan, 1981). Nymphs are similar in body shape to the adults (Plate 3-11). Nymphs of insidious flower bugs are yellowish in the first, second, and third stage and have a distinct orange dorsal scent gland on the third, fourth, and fifth abdominal segments; the fourth and fifth stage nymphs are tan to dark brown (Isenhour and Yeargan, 1981). Newly emerged nymphs of the minute pirate bug are shiny and almost colorless, but become greenish yellow after a few hours; sometimes in the fourth and mainly the fifth nymphal stage, the dorsal abdominal segments become dark brown (Askari and Stern, 1972).

Developmental time of the insidious flower bug and the minute pirate bug is influenced by type of food and rearing conditions (Isenhour and Yeargan, 1981; Kiman and Yeargan, 1985; Askari and Stern, 1972; Salas-Aguilar and Ehler, 1977) (Table 3). The

Table 3. Time of development for the insidious flower bug and minute pirate bug as affected by temperature.

Species	Temperature F (C)	Average number of days required for completion of the indicated stage	
		Egg	Nymph
Insidious flower bug[1]	68.0 (20)	8.8	24.8
	75.2 (24)	5.1	14.9
	82.4 (28)	3.9	8.7
	89.6 (32)	3.5	8.6
Minute pirate bug[2]	70.0 (21.1)		26.4
	77.9 (25.5)	3-5	14.4
	92.0 (33.3)		8.4
	68.0 (20)	6.0	17.1
	77.0 (25)	3.8	14.7
	86.0 (30)	3.0	11.8
	95.0 (35)	2.5	9.9

[1]From Isenhour and Yeargan (1981); fed eggs of tobacco budworm (frozen for one hour prior to feeding) and water.

[2]From Askari and Stern (1972); fed Pacific spider mites, *Tetranychus pacificus* McGregor, and lima beans. Also from Butler (1966b); fed green beans or alfalfa leaves and alfalfa leaves infested with twospotted spider mites, *Tetranychus urticae* Koch.

developmental period at 75.2F (24C) from oviposition to adult eclosion for the insidious flower bug fed frozen tobacco budworm eggs and water was 20 days and as short as 12 days at 84.4 (28C) and 89.6 (32C) (Isenhour and Yeargan, 1981). Using a similar temperature [77F (25C) or 77.9 (25.5C)] but with different food (Pacific spider mites, *Tetranychus pacificus* McGregor or twospotted spider mites, *Tetranychus urticae* Koch), Askari and Stern (1972) and Butler (1966b) reported that development from the egg to the adult took about 18.5 days for the minute pirate bug. The insidious flower bug requires slightly longer to complete development than the minute pirate bug (Isenhour and Yeargan, 1981). Kiman and Yeargan (1985) evaluated the effect of several diets made up singly or of different combinations of frozen tobacco budworm eggs, maple pollen, green beans, adult soybean thrips, *Sericothrips variabilis* (Beach), or twospotted spider mites with free water on insidious flower bug and found that diets that included tobacco budworm eggs alone or in combination were optimum for survival, developmental time, longevity and fecundity. Also, survival to the adult stage was possible with all the diets except green beans and water alone. The ability of the insidious flower bug to complete development on different types of prey (moth eggs, mites and thrips) and on pollen alone is important. Evaluations with the minute pirate bug indicate that it is able to complete development on green beans alone and on pollen and water (Salas-Aguilar and Ehler, 1977). It is very significant that both species can complete development on a diet of pollen and water alone.

The preoviposition period for adult females is two to five days for both species. Laboratory studies indicate an adult longevity of about one month. Average fecundity for females fed optimum diets is about 100 eggs per female. Barber (1936) reported that female insidious flower bug feeding on bollworm eggs oviposited an average of 114 eggs each while Kiman and Yeargan (1985) found that females reared on diets containing tobacco budworms eggs oviposited 102 to 106 eggs per female. For the minute pirate bug, Askari and Sterns (1972) found an average fecundity of 129 eggs per female on a diet of Pacific spider mites and lima beans. However, Salas-Aguilar and Ehler (1977) reported an average fecundity of 59.6 eggs per female and a total longevity of 15.4 days on a diet of beans, pollen, thrips and free water.

Iglinsky and Rainwater (1950) suggested that the insidious flower bug is more likely to overwinter as a mature, mated female. Whitcomb and Bell (1964) reported that this species overwinters in the adult stage in plants such as wheat, alfalfa, grasses, mullein and henbit and become active on warm days. Kingsley and Harrington (1982) verified that insidious flower bug adults undergo a facultative reproductive diapause which is apparently terminated by favorable conditions during the spring, but that does not require an interval of cold exposure for diapause development. They also reported that the females mated before overwintering.

Major concerns relative to the importance of *Orius* spp. (flower bugs) as predators in cotton are timing of colonization, sources of colonizers during the season, ability to become established and reproduce in cotton and predatory efficacy. Flower bugs are early season colonizers of cotton and apparently are attracted by thrips and spider mites which develop during the early season (van den Bosch and Hagen, 1966;

Bohmfalk *et al.*, 1983; Smith and Stadelbacher, 1978). The sources for these early colonizers are likely winter crops and weeds. A major source of colonizer *Orius* spp., specifically the insidious flower bug may be field corn. The insidious flower bug has an affinity for silking corn and is able to reproduce very effectively in this crop while feeding on pollen and noctuid eggs (Quaintance and Brues, 1905; Barber, 1936). Movement of the insidious flower bug from corn to cotton occurs during mid-season after the corn is mature, and when bollworms also move from corn to cotton. High mortality as a consequence of insecticide applications may reduce the potential value of this predator at this time because it appears to be very susceptible to commonly used insecticides. The minute pirate bug and insidious flower bug apparently have the greatest impact in early to mid-season (Wene and Sheets, 1962, Smith and Stadelbacher, 1978).

Both species are important predators of thrips, mites, aphids, whiteflies and especially of eggs and small larvae of noctuids and other moth species in cotton (Ewing and Ivy, 1943; Fletcher and Thomas, 1943; Iglisky and Rainwater, 1950; Whitcomb and Bell, 1964; Bell and Whitcomb, 1964; van den Bosch and Hagen, 1966; Whitcomb, 1967; Ehler *et al.*, 1973; Ridgway and Lingren, 1972; McDaniel *et al.*, 1981; McDaniel and Sterling, 1982). Fletcher and Thomas (1943) identified insidious flower bugs as having preyed on the greatest percentage of bollworm eggs and larvae on cotton. McDaniel *et al.* (1981) and McDaniel and Sterling (1982) detected radioactive insidious flower bug nymphs and adults that had fed on radioactive eggs and first and second instars of bollworm/tobacco budworm placed in cotton. Adults of insidious flower bug consumed a mean of 0.7 and 4.4 eggs and first instar bollworms per predator per day, respectively, in laboratory studies (Lingren *et al.*, 1968). In California, the minute pirate bug is an important part of the natural enemy complex influencing bollworm, cabbage looper, and beet armyworm abundance in cotton (Ehler *et al.*, 1973; Eveleens *et al.*, 1973; van den Bosch and Hagen, 1966). As predators of the pink bollworm, the minute pirate bug preferred first instars over eggs (Henneberry and Clayton, 1985; Orphanides *et al.*, 1971).

Factors that may impact on the ability of flower bugs to colonize cotton involve the interaction between the cotton plant, prey available on the plant and the predator itself. Significant reductions in the numbers of insidious flower bug were found in nectariless and pilose cotton compared to more typical cotton varieties (Schuster *et al.*, 1976; Shepard *et al.*, 1972). Higher numbers of flower bugs were closely associated with higher numbers of mites and thrips (Yokoyama, 1978; Stoltz and Stern, 1978; Gonzalez and Wilson, 1982) on cotton plants in the San Joaquin Valley. The highest proportion of minute pirate bug nymphs was found on fruit during peak squaring. Adults were found higher on the plant than the nymphs, and there was a predominance of this species close to the plant terminal (Wilson and Gutierrez, 1980).

Ants—Although many predators feed on bollworms, tobacco budworms and cotton fleahoppers, ants, specifically fire ants, *Solenopsis* spp., are the only ant predators in cotton fields that play a significant role in the suppression of these key pests included

in the TEXCIM model (Hartstack and Sterling, 1989; Hartstack *et al.*, 1990). Fire ants are also important predators of the cotton leafworm (Gravena and Sterling, 1983). Other predator groups such as green lacewings may be important predators of both bollworm/tobacco budworm and/or cotton fleahoppers but not boll weevils. For the characteristics needed for identification of the species of *Solenopsis*, see Hung *et al.* (1977).

The red imported fire ant, *Solenopsis invicta*, appears to be the most important species of fire ants in cotton agroecosystems of the United States because of its distribution, abundance and predatory aggressiveness. It is currently distributed over the southeastern United States from North Carolina to central Texas (Vinson and Sorensen, 1986) which constitutes a large portion of the Cotton Belt. Its geographical distribution is thought to be limited primarily by physical factors (Lofgren *et al.*, 1975). To the north it is limited by the zero degree Fahrenheit isotherm (Pimm and Bartell, 1980) and to the west by dry, desert conditions (Tschinkel, 1982). Red imported fire ants can become very abundant under certain conditions, approaching 2500 small colonies per hectare (Lofgren *et al.*, 1975).

The black imported fire ant, *Solenopsis richteri* Forel, is currently found only in northeast Mississippi and northwest Alabama, but may ultimately spread into northern Arkansas, Georgia and southern Tennessee (Vinson and Sorenson, 1986). Little is known of its predatory impact on the pests of cotton.

The tropical fire ant, *Solenopsis geminata* (F.), occupies a geographical distribution in the United States ranging from Texas to South Carolina along coastal regions. It is probably the most common fire ant species in the Rio Grande Valley of South Texas and into Mexico. Its biology is similar to the red imported fire ant (Vinson and Greenberg, 1986).

The last fire ant to be considered here is the southern fire ant, *Solenopsis xyloni* McCook, which can be found inland from California to North Carolina (Vinson and Greenberg, 1986). Where the mound of the other species tends to be elevated, the southern fire ant mound is flat.

Individuals of these four species of ants are considered to have an equal impact as predators of plant-feeding insects in cotton fields to simplify assessment. Thus, a tropical fire ant worker is considered to be equal to a red imported fire ant worker as a predator of cotton fleahoppers, bollworms/tobacco budworms or boll weevils. However, as a species, the red imported fire ant likely has a much greater impact on plant feeding insects in cotton than the other three species. Also, in areas occupied by the red imported fire ant, the other species have largely been displaced (Hung *et al.*, 1977).

The *Solenopsis* species are lumped into a group referred to as "fire ants" during the remainder of this paper. However, there is a paucity of information of the predatory impact of the species other than the red imported fire ant. It safely can be assumed that there are some differences in the biologies and predatory impacts of the species; however, until the importance of these differences are clear, an assumption of similarity is made. Even within a species, there may be differences between colonies. Some of the

red imported fire ant colonies have multiple queens and some have single queens. The worker ants from a single queen colony forage out and back into the same mound. Worker ants from multiple queen colonies may forage out of one mound into a second mound which functions as a "supercolony" (Bhatkar, 1988). A major difference is that single queen colonies vary in density from 15 to 80 mounds per acre compared to 130 to 500 mounds per acre with multiple queen colonies. This difference in behavior by ants from different colonies ultimately may prove to have an important impact on the efficacy of ants as predators.

The biology and ecology of red imported fire ants has been reviewed by Lofgren *et al.* (1975), Lofgren (1986), and Vinson and Greenberg (1986). One of the main ways that fire ants disperse is through mating flights. Since these ants select locations for mound building that will be exposed to sunlight (Bhatkar, 1989), such as crop land and pastures, they quickly colonize and occupy recently planted cotton fields. Colonization of a cotton field takes place through the foraging of workers from colonies outside the cotton field and from new queens after a mating flight. Mated queens may fly up to 12 miles (Banks *et al.*, 1973) or more than 20 miles (Wojcik, 1983) and thus, can easily colonize large cotton fields rapidly. However, new queens produce only mini (very small) workers (Fincher and Lund, 1967) which are unlikely to have a major impact as predators of cotton pests. More than a month may be required before a newly colonized queen will begin to produce the minor workers needed for predation of pests. The worker ants that colonize cotton fields from established colonies outside the cotton field consist of minor and major workers that readily attack and kill cotton fleahoppers, bollworm/tobacco budworm and boll weevils (Hartstack and Sterling, 1989). Colonization of cotton fields by old colonies is triggered by several factors including the attraction of worker ants to aphid honeydew (Nielsson *et al.*, 1971), and cotton plant nectar (Agnew *et al.*, 1982). However, its primary diet and attractant consists of insects and other small invertebrates (Wilson and Oliver, 1969).

Though fire ants are polyphagous (feed on many kinds of food) predators, they do not pauperize the entire predator and parasite arthropod populations of cotton fields (Sterling *et al.*, 1979). Of course, ants can kill individuals of many species of natural enemies such as the parasites *Cardiochiles nigriceps* (Lopez, 1982) and *Bracon mellitor* Say (Sturm, 1989; Sturm and Sterling, 1990), and predaceous ground beetles (Brown and Goyer, 1982). Though these statements may seem contradictory (Lofgren, 1986), there is a distinct difference between "pauperizing a fauna (animal life inhabiting a specific environment)" and killing some individuals of a species. To pauperize a fauna, certain species are either eliminated or dramatically reduced in abundance due to some factor. To be able to claim that ants have a major impact on a species of parasite or predator, detailed life tables of the parasite or predator that clearly show the impact of ants are necessary. There should be clear evidence of indispensable mortality (Southwood, 1978) due to the ants on the parasites, similar to that shown for ants on boll weevils by Sturm *et al.*, (1989). Another source of convincing evidence of the impact of a natural enemy is produced by models such as TEXCIM that can predict the dynamics of pests based on counts of natural enemies (Sterling *et al.*, 1993).

Cotton Fleahoppers. Breene *et al.* (1990), in laboratory studies demonstrated the importance of the red imported fire ant as a predator of the cotton fleahopper. The predation rate was described as a function of both ant and cotton fleahopper abundance. At the highest ant density, 100 percent of the fleahoppers were killed in 24 hours. Field evidence of predation on fleahoppers by these ants is provided by Breene *et al.* (1988, 1989a) who found radiolabeled ants after field releases of radiolabeled fleahoppers. This predation takes place primarily at night so that it is infrequently observed during the day under field conditions.

Bollworm/Tobacco Budworm. Radiolabeled bollworm/tobacco budworm eggs and larvae were released in East Texas and the imported fire ant was shown to be a key predator of eggs (McDaniel and Sterling, 1979, 1982) and larvae (McDaniel *et al.*, 1981) (Plate 3-12). The rate of egg predation by ants is partially a function of temperature (Agnew and Sterling, 1982).

Boll Weevils. Fire ants are the only key predators of immature boll weevils (Sterling, 1978; Sterling *et al.*, 1984). These ants primarily attack immature boll weevils while they are feeding inside squares (flower buds) (Sturm and Sterling, 1986). They also attack immatures and soft adults in pupal cells when a boll splits at maturation (Agnew and Sterling, 1981). The hard exoskeleton of the adult boll weevil provides an excellent defense against ant predation so the impact of ants on adult weevils is minimal. The limitations of predation by fire ants is that they generally do not enter green squares on the plant nor do they enter green bolls before they split in search of boll weevils. However, after the square has dropped to the soil surface and has begun to decompose, ants readily chew a hole, enter and kill the weevil inside (Sturm, 1989; Sturm and Sterling, 1986; Sturm *et al.*, 1989, 1990).

In Texas, the rate of predation on cohorts of boll weevils ranges from 0 percent in western Texas where fire ants are absent to 100 percent in fields of eastern Texas where ants are abundant (Fillman and Sterling, 1983; Sturm and Sterling, 1990; Sturm *et al.*, 1989). The red imported fire ant is a major boll weevil mortality agent in East Texas and has its greatest impact during August (Sturm and Sterling, 1990; Sturm *et al.*, 1990). These ants are not equally abundant from field to field, thus cannot automatically be depended on for weevil control. However, in fields where they are abundant, cotton can be grown without insecticidal control of boll weevils, especially if delayed planting and early stalk destruction practices are employed (Sturm *et al.*, 1990). During an eleven year period, higher average yields were obtained in unsprayed plots containing ants than in plots where insecticides were used to control cotton pests (Sterling *et al.*, 1984). Ant predation was a key mortality factor of the boll weevil in eastern coastal regions of Texas (Fillman and Sterling, 1983; Sturm *et al.*, 1990). A density of 0.4 ants per plant was sufficient to control boll weevils 90 percent of the time (Fillman and Sterling, 1985). The removal of ants from cotton fields resulted in the resurgence of boll weevils compared to fields where ants were undisturbed (Sterling, 1984; Sterling *et al.*, 1989).

Fire ants are one of the ten groups of predators used by TEXCIM (Sterling *et al.*, 1993) to predict the phenology and abundance of pests in cotton. This model uses field

counts of these ten groups of predators to forecast the abundance and economics of bollworms, tobacco budworms, cotton fleahoppers, and boll weevils and their multi-pest economics. The TEXCIM model (Sterling *et al.*, 1993) can be used to forecast the economic benefits of ant predation and the desiccation of boll weevil larvae in abscised (fallen) squares as well as the cost of boll weevil injury. This model is based on a detailed understanding of the biology and ecology of the boll weevil, its interaction with the cotton plant, and its interaction with other herbivorous (plant-eating) species and natural enemies.

Although fire ants sting humans, damage some crops, and short out electrical systems (Lofgren *et al.*, 1975; Lofgren, 1986; Vinson and Sorensen, 1986), they also are important natural enemies of some very important pests such as boll weevils, bollworms, tobacco budworms, fleahoppers, ticks, and sugarcane borers (Sterling *et al.*, 1979). Thus, it is not accurate to label fire ants as either pests or beneficial insects without qualification because under some conditions they cause more harm than good while in others, such as in cotton fields, they may make a profitable contribution. Fire ants can be "beneficial or harmful to the same plant or animal species depending on the time of year and/or developmental stage of the species, environmental conditions, or the status of the ant colony itself" (Lofgren, 1986).

SPIDERS

The ecological role of spiders in the suppression of cotton pests has been the subject of debate in the face of a large shortage of data. The theory of spiders as biological control agents has been dealt with by Riechert and Lockley (1984) who have expressed concern that biological control efforts have been more concerned with "putting out fires" rather than preventing them. They conclude that no single spider species can hold a prey in check and that even an assemblage of spider species can have little more than a "buffering effect". The argument prevails that spiders are generalist predators and do not form a tight linkage (i.e., prey specificity) in a density-dependent fashion with any particular prey species. Data by Nentwig (1986) however, contradict this notion since he found several species that were prey specialists. Most spiders have only about one generation per year, and have no way of increasing their numbers in response to prey density by local reproduction (Turnbull, 1973). However, spiders may respond to increased prey density by shrinking their searching territories, by recruitment and by colonization (Goodenough *et al.*, 1986). Thus, it generally has been concluded that spiders can maintain prey at low densities but they are largely incapable of reducing the abundance of outbreaks. We think that this conclusion tends to overgeneralize and that, until the true role of more spider species is known, it is premature to come to conclusions about spiders as a group. There is evidence that some spiders when operating in conjunction with other mortality factors, can not only maintain low prey populations but can also suppress them below economically damaging levels. Spiders have played a role in the reduction of crop damage in apple orchards (Mansour *et al.*, 1980), in sorghum (Horner, 1972; Muniappan and Chada, 1970a), and in rice (Kiritani *et al.*, 1972; Kiritani and Kakiya, 1975).

The evidence that spiders play a role in the dynamics of pest species in the cotton ecosystem is still patchy and far from complete. There is an abundance of studies in other agroecosystems as reviewed by Nyffeler (1982) and Nyffeler and Benz (1987). A considerable body of work dealing with the identification or feeding ecology of spider inhabitants of cotton fields is available (Dean and Sterling 1987; Lockley and Young, 1987; Nyffeler *et al*., 1986, 1987a, b, c, 1988, 1989; Whitcomb and Bell, 1964; Young and Lockley, 1985, 1986). Whitcomb and Bell (1964) identified 160 species of spiders in Arkansas cotton fields while Dean *et al*., (1982) identified 97 species in East Texas and Leigh and Hunter (1969) found 34 species in California and Skinner (1974) observed 154 species in Alabama and Mississippi cotton fields. Young and Edwards (1990) listed 308 species found on cotton in the United States. Many species found in cotton fields are only temporary residents. However, other species frequently are found in fairly large numbers and over broad geographical areas. Dean and Sterling (1987) observed that crab spiders, *Misumenops* spp., striped lynx spiders, *Oxyopes salticus* Hentz, and long-jawed orb weavers, *Tetragnatha laboriosa* Hentz were among the most abundant taxa of spiders in cotton throughout Texas. In general, about half of the predaceous arthropods in cotton are spiders (Fuchs and Harding, 1976). Because of the number of species of spiders considered important in cotton, it is only possible here to present a general review of the group and to cite sources where more specific information can be obtained. Roth (1993) provides keys and taxonomic differences for the identification of spider species found in the United States. Breene *et al*. (1993) discuss the biology, predation ecology, and significance of the 146 spider species collected from cotton in Texas and include a key and illustrations of the spiders.

The studies that have been conducted are important to our understanding of spider dynamics and feeding habits, but provide limited evidence of spider impact on key pests of cotton. Dean and Sterling (1987) reported that overall, spiders may have a positive or negative effect depending on whether they are feeding primarily on pests or other predators.

Cotton Fleahoppers. Twenty-two spider species are known to prey on the cotton fleahopper (Dean *et al*., 1987). Though some insect predators prey on fleahoppers, spiders apparently play a dominant role in suppression of the cotton fleahopper (Breene *et al*., 1989b). However, some of these species are of much greater importance than others. The studies of Dean *et al*. (1987), Breene and Sterling (1988) and Breene *et al*. (1988, 1989a, b, 1990) indicate the most important spider predators of the cotton fleahopper in Texas (Table 4).

The striped lynx spider generally constitutes the most important predator of the cotton fleahopper (Plate 3-13). In East Texas, the striped lynx spider comprised 23 percent of all spiders collected in cotton (Dean *et al*., 1982) and was abundant throughout Texas (Dean and Sterling, 1987). It also dominates in soybean and cotton ecosystems in Mississippi (Pitre *et al*., 1978). The striped lynx spider has a somewhat limited prey range and apparently shows some preference for members of the Heteroptera and Homoptera because 71 percent of its prey items belong to these orders (Lockley and Young, 1987). This spider is an active leaper and can be recognized by eight eyes in

Table 4. Spider predators of the cotton fleahopper in Texas.[1]

Groups (Family) and Species	Index of efficacy for fleahoppers	
	Nymphs	Adults
Jumping spiders (Salticidae)	0.9	0.9
Metaphidippus galathea		
Hentzia palmarum		
Phidippus audax (black and white jumping spider)		
Lynx spiders (Oxyopidae)	0.7	0.7
Oxyopes salticus (striped lynx spider)		
Peucetia viridans (green lynx spider)		
Cheiracanthium inclusum (winter spider)		
Crab spiders (Thomisidae)	0.5	0.4
Misumenops celer (celer crab spider)		
Web spinning spiders	0.4	0.3
Grammonota texana		
Tetragnatha laboriosa (long-jawed orb weaver)		

[1]From Breene *et al.* (1989a) and Hartstack et al. (1991). A value of 1.0 would have the highest efficiency rating against the cotton fleahopper while a value of 0 would indicate no efficacy. The index values relate to the consumption rates of cotton fleahopper by these spider groups.

the form of a hexagon on the carapace (the top part of the head and thorax), large spines on the legs, and a black stripe on each of the chelicerae (first pair of appendages of the head that are used as jaws; they terminate with fangs that are used to help catch prey) and with four longitudinal gray bands on the carapace. The female averages 1/4th inch (5.9 millimeters) in length and the male, about 1/5th inch (4.7 millimeters). There are one to two generations per year. Other features of its biology are available from Whitcomb and Eason (1967). It is found in many habitats (including crops), but primarily in grassy areas; it is found throughout the Cotton Belt (Young and Lockley, 1985). Overwintering occurs in the second to seventh instar but adults can be found year-round in warmer areas. Dispersal, which is mostly accomplished by earlier instars, is achieved by ballooning, a method spiders use to "fly" through the air on a strand of silk from their spinnerets (located at the end of their abdomen).

The green lynx spider, *Peucetia viridans* (Hentz), which is found throughout the Cotton Belt, is one of the largest spiders in cotton fields and consumes large numbers of cotton fleahoppers (Nyffeler *et al.*, 1987a). Females average about 5/8ths inch (16.2 millimeters) in length and the males, about 1/2 inch (11.9 millimeters). The eyes and legs are similar to that for the striped lynx spider but the green lynx is green in color and is larger. There is one generation per year. Details of its life history are available from Whitcomb *et al.* (1966). It is usually the larger instars that move into cotton in June and July.

The winter spider, *Cheiracanthium inclusum* (Hentz), is not a true lynx spider but is placed in this group because it has a similar efficiency rating to the lynx spiders (Plate

3-14). It has one (possibly two) generation(s) per year and overwinters as a late instar or adult. Distinguishing characters include two rows of eyes, a lanceolate mark on the abdomen, and is cream colored to light brown (occasionally pale yellow to pale green). The female is about 9/32nds inch (7.2 millimeters) long and the male is 15/64ths inch (5.8 millimeters). It is nocturnal (active at night) and hides during the day in tube webs in the tips of rolled leaves or bracts of cotton fruit. It is widely distributed and feeds on a wide range of prey. Peck and Whitcomb (1970) studied the biology.

Crab spiders are ambush predators that sit and wait in the terminals of cotton plants (Plates 3-15 and 3-16). They are the most abundant taxa of spiders in the western part of Texas (Dean and Sterling, 1987). Muniappan and Chada (1970b) reported on the biology of *Misumenops celer* (Hentz). They can be recognized by their crab-like first two pairs of legs, which are the longest. The females are about 11/64ths to 17/64ths inch (4.4 to 6.7 millimeters) in length and the males are about 1/16th to 5/32nds inch (1.5 to 4.0 millimeters). There are one to two generations per year. They are found in many types of habitats and have a variable diet.

Jumping spiders (family Salticidae) prefer to attack prey with high activity levels and crawling velocities (Freed, 1984) (Plate 3-17). However, jumping spiders will also prey on sessile prey (prey that do not move about) such as bollworm eggs (McDaniel and Sterling, 1979, 1982). They have three rows of eyes with the eyes in front the largest. They have a compact rectangular body with stout legs. The size of the adult ranges from about 1/8th to 19/32nds inch (3 to 15 millimeters) in length depending on the species. The color varies greatly from light to irridescent to black with combinations of colors. There generally is one generation per year and they overwinter as late instars and adults. They are found in many habitats and are widespread across cotton growing areas.

Web spinners (families Araneidae and Tetragnathidae) vary greatly in color, size [5/64ths to 1 and 1/10th inches (2 to 28 millimeters) in length], and shape but all make some type of web (orb, tangled, or in-between) to capture various types of prey. More than two-thirds of all orb weavers in cotton in Texas consist of five species: star-bellied orb weaver, *Acanthepeira stellata* (Walckenaer); *Neoscona arabesca* (Walckenaer), *Gea heptagon* (Hentz); long-jawed orb weaver, *Tetragnatha laboriosa* Hentz; and, feather-legged spider, *Uloborus glomosus* (Walckenaer). More than 99 percent of their prey consists of insects, (mostly aphids) and less than 1 percent being spiders (Nyffeler *et al*., 1989).

Bollworm/Tobacco Budworm. Spiders feed readily on bollworm/tobacco budworm eggs, larvae, and adults (McDaniel *et al*., 1981; McDaniel and Sterling, 1982; Whitcomb, 1967). Their impact on these species is less certain than their impact on the cotton fleahopper and it depends on the abundance and efficacy of the various spider species (Hartstack and Sterling, 1989). Although most of the evidence of spider predation is on bollworm/tobacco budworm larvae, the green lynx spider has also been observed seizing bollworm and cotton leafworm moths (Whitcomb and Bell, 1964).

Boll Weevils. The impact of spiders on the boll weevil is limited to the reports of Whitcomb and Bell (1964) that the black and white jumping spider, *Phidippus audax*

(Hentz), has been observed feeding on an adult boll weevil in the field. They also observed spiders of the family Lycosidae including the wolf spiders *Gladicosa gulosa* Walckenaer, *Hogna punctulata* (Hentz) and *Varacosa avara* (Keyserling) feeding on boll weevil adults in the laboratory. However, there are other species capable of feeding on this pest. Black widow spiders, *Latrodectus mactans* (Fabricius), feed readily on the legs of beetles. These spiders have very small mouthparts so that they are only able to suck the body fluids of large prey through their legs. Also, the green lynx spider has been observed to feed on an adult boll weevil in the field (Breene *et al.*, 1993). However, there is currently no evidence that any spider species can kill immature boll weevils within the fruit.

Other Cotton Insects. Radiolabeled pink bollworm moths were killed by the following three spiders: wolf spider, *Pardosa milvina* (Hentz), jumping spider, *Plexippus paykulli* (Audouin), and black and white jumping spider according to Clark and Glick (1961). Thus, it is very likely that spiders also feed on other adults of cotton pests such as cotton leafworms. Nine spider species were observed to feed on pink bollworm larvae in southern California (Orphanides *et al.*, 1971). Eggs of the cotton leafworm are fed upon by green lynx spiders, winter spiders, gray dotted spiders, *Hibana (=Aysha) gracilis* (Hentz) and the orb weaver spider, *Neoscona arabesca* and first instar larvae were fed on by crab spiders, long-jawed orb weavers, gray dotted spiders, green lynx spiders, winter spiders, and the jumping spider, *Hentzia palmarum* (Hentz) and an erigonid (Gravena and Sterling, 1983). The cotton leafperforator, *Bucculatrix thurberiella* Busck, is attacked frequently by spiders of the genera *Theridion* and *Theridula* of the family Theridiidae which are commonly called comb-footed spiders, in cotton fields in northern Peru (Herrera and Alvarez, 1979). Spiders were able to suppress larval infestations of Egyptian cotton leafworm, *Spodoptera littoralis* (Boisduval), in Israel (Mansour, 1987).

Nyffeler (1982) has suggested that because spiders eat other predators that they do as much harm as good in cotton fields. If this is a valid criticism of spiders, then it also applies to many of the insect predators. Predaceous insects and spiders are generally polyphagous. In one sense, having a wide prey range is beneficial in that these predators can switch to other prey when a preferred prey becomes rare so that it is not necessary for them to leave the cotton field to prevent starvation (Murdoch, 1969).

ECONOMIC IMPACT OF PREDATORS

Using the TEXCIM model it is possible to retrospectively estimate the value of predators of cotton fleahoppers, boll weevils, or bollworms and tobacco budworms. An example (Table 5) shows values of fleahopper predators for five years in untreated cotton fields in East Texas. As a group, web spinning spiders had the greatest average economic impact [$1.78 per acre ($4.40 per hectare)] over the growing season. Lynx spiders [$1.47 ($3.63)] were next, followed by red imported fire ants [$1.06 ($2.62)], predaceous bugs [$0.40 ($.99)], crab spiders [$0.38 ($.94)] and jumping spiders [$0.34 ($0.84)].

Care must be exercised in interpreting these values. A farmer using no insecticides would make an average profit of $5.44 ($13.44 per hectare) more per acre with preda-

tors than without them. This does not mean that using predators is always more profitable than using insecticides for fleahopper control. It means that the value of predators must be taken into account when deciding whether to use insecticides if all costs and benefits are taken into consideration in making management decisions.

Table 5. Value ($) of predators of the cotton fleahopper for the indicated years.[1]

Predators	1978	1979	1980	1981	1989	Average
Fire ants	1.09	0.37	0.14	3.58	0.13	1.06
Lynx spiders	0.85	0.48	0.11	5.39	0.54	1.47
Jumping spiders	0.48	0.13	0.18	0.51	0.38	0.34
Crab spiders	0.66	0.08	0.11	0.34	0.71	0.38
Web spinning spiders	1.12	1.47	0.22	5.21	0.90	1.78
Predaceous bugs	0.48	0.08	0.10	0.47	0.87	0.40
Total	4.68	2.61	0.86	15.50	3.53	5.44

[1]From Sterling et al. (1992).

PARASITES

Although a number of parasite species associated with the cotton insect pest complex have been identified, the emphasis in our discussion is on important parasite species of bollworm/tobacco budworm. These pests are attacked by numerous species of wasp and fly parasites (Table 6). The most important wasp parasites, in terms of number of hosts parasitized, appear to be *Microplitis croceipes*, *Cardiochiles nigriceps* and *Trichogramma* spp. Some of the more important fly parasites are *Archytas marmoratus* and *Eucelatoria bryani*. These parasites will be discussed in the following pages.

WASPS

Microplitis croceipes—One of the most important wasp parasites of bollworm/tobacco budworm larvae is *Microplitis croceipes*, an endoparasitic (develops inside the host) braconid. This parasite is found from New Jersey to Georgia and west to New Mexico, Arizona, Utah and Oregon (Muesebeck *et al.*, 1951; Marsh, 1978). This parasite is common in Mississippi throughout the cotton growing season (Lewis and Brazzel, 1968) and is reported to be active over a longer period of time than any other parasite attacking *Helicoverpa/Heliothis* (Stadelbacher *et al.*, 1984). Apparently *Microplitis croceipes* does not occur in California (van den Bosch and Hagen, 1966). *Microplitis croceipes* attacks the bollworm, tobacco budworm and *Heliothis subflexa* (Guenee), and is among the most common and important parasites of bollworm/tobacco budworm larvae in the United States (Quaintance and Brues, 1905; Lewis and Brazzel, 1966, 1968; Snow *et al.*, 1966; Bottrell *et al.*, 1968; Neunzig, 1969; Lewis and Snow, 1971; Young and Price, 1975; Smith *et al.*, 1976b; Marsh, 1978; Danks *et al.*, 1979; Eger *et al.*, 1982; Powell and Elzen, 1989). It often

Table 6. List of representative parasites attacking bollworm/tobacco budworm in the United States.

Group	Family	Species
Wasps[1]:		
	Braconidae	
		Bracon platynotae (Cushman)
		Cardiochiles nigriceps (Vierick)
		Chelonus insularis (Cresson)
		Cotesia marginiventris (Cresson)
		Meteorus autographa Muesebeck
		Meteorus laphygmae Vierick
		Microplitis croceipes (Cresson)
		Microplitis feltiae Muesebeck
		Rogas perplexus Gahan
	Eulophidae	
		Euplectrus platyhypenae Howard
	Ichneumonidae	
		Campoletis flavicincta (Ashmead)
		Campoletis sonorensis (Cameron)
		Cryptus albitarsis (Cresson)
		Hyposoter annulipes (Cresson)
		Netelia sayi (Cushman)
		Netelia spinipes (Cushman)
		Pristomerus spinator (Fabricus)
	Scelionidae	
		Telenomus heliothidis Ashmead
	Trichogrammatidae	
		Trichogramma spp.
Flies[2]		
	Tachinidae	
		Archytas marmoratus (Townsend)
		Carcelia illota (Curran)
		Eucelatoria armigera (Coquillett)
		Eucelatoria bryani Sabrosky
		Euphorocera claripennis (Macquart)
		Euphorocera floridensis Townsend
		Euphorocera tachinomoides Townsend
		Gonia spp.
		Gymnochaetopsis fulvicauda (Walton)
		Hyphantrophaga hyphantriae (Townsend)
		Lespesia aletiae (Riley)
		Lespesia archippivora (Riley)

Table 6. Continued

Group	Family	Species
		Lespesia frenchii (Williston)
		Metaplagia occidentalis Coquillett
		Nemorilla pyste (Walker)
		Palexorista laxa (Curran)
		Voria aurifrons (Townsend)
		Winthemia quadripustulata (Fabricius)
		Winthemia rufopicta (Bigot)

[1]Data from Krombein et al. (1979).
[2]Data from Arnaud (1968).

parasitizes more than 50 percent of the individuals that survive to reach the larval stage in field populations (Mueller and Phillips, 1983; Stadelbacher *et al.*, 1984; King *et al.*, 1985). Mueller (1983) reported that, although *Microplits croceipes* females did not distinguish between bollworms, and tobacco budworms, parasite survival was higher in bollworms than in tobacco budworms.

Adult *Microplitis croceipes* are large dark brown to black wasps, with yellow to reddish abdomen (darker posteriorly) and legs (Plate 3-18). The wings are rather dark. The female has a short ovipositor and antennae that are shorter [about 5/32nds inch (4 millimeters)] than those of the male [about 15/64ths inch (6 millimeters)].

Microplitis croceipes has three larval instars (Lewis, 1970a). The egg hatches from 36 to 48 hours after oviposition. The first instar larval stage lasts for approximately four days, the second instar for about three days, and the third instar for about one day. The pupal stage inside the cocoon lasts for approximately six days, or the insect may remain in diapause, in the prepupal stage inside the cocoon for a variable period of time. Under field conditions, the cocoons are found underground in a tunnel excavated by the parasitized host larva. Prepupae are induced into diapause by low temperatures (Powell and Elzen, 1989). Diapause inducement at 59, 68 and 86F (15, 20, and 30C) was 100, 60 and zero percent, respectively. Short daylengths cause a higher rate of diapause induction with appropriate temperatures. It took an average of 9 to 11 days for fully developed parasite larvae to emerge from the host, depending on the developmental stage of the host at oviposition (Lewis, 1970b).

Although all bollworm and tobacco budworm (host) larval stages are subject to attack, *Microplitis croceipes* females preferentially attack third instar bollworm and tobacco budworm larvae (Lewis, 1970b; Hopper and King, 1984). First and second instar larvae are so small that they are difficult to find while fourth and fifth instars are so large that they can dismember the parasites with their mandibles (Herman and Morrison, 1980). Late fifth instar larvae (prepupae) are unsuitable as hosts and produce no parasites if they are accepted for oviposition (Lewis, 1970b). After parasitization, host larvae continue normal development to the fourth or fifth instar before the parasite larvae emerge. Hopper and King (1984) determined that bollworm/tobacco

budworm larvae parasitized as second, third, and fourth instars moved less and damaged fewer squares, blooms, and bolls than unparasitized larvae.

Microplitis croceipes is very host specific. Bollworm/tobacco budworm larvae, however, attack numerous plant species. Thus, the role of plants in the host selection behavior of this parasite is very important. *Microplitis croceipes* has been reported to attack bollworm/tobacco budworm in many cultivated crops, including alfalfa, beans, cotton, tobacco, tomato, corn and sorghum (Bottrell *et al.*, 1968; Butler, 1958; Burleigh, 1975; Lewis and Brazzel, 1966; Neunzig, 1969; Shepard and Sterling, 1972a; Smith *et al.*, 1976b; Young and Price, 1975; Powell and King, 1984). Parasitization in corn and sorghum is extremely low (Lewis and Brazzel, 1968; Neunzig, 1969; Smith *et al.*, 1976b). Stadelbacher *et al.* (1984) report that *Microplitis croceipes* parasitized bollworm/tobacco budworm larvae on more species of plants, in Mississippi, than any other parasite.

Mueller (1983) studied the survival of *Microplitis croceipes* in nine host insect/plant combinations and found that survivorship was higher in host larvae that were reared on cotton than in hosts reared on either bean or tomato. Thus, the plant on which a larva feeds also can be an important factor in determining the probability of successful parasitism by this species. The availability of nectar on the cotton plant has been determined to affect the longevity and fecundity of the adult parasite (Calderon, 1977). Mean adult longevity was one day less and fecundity was reduced by 49 percent on nectariless cotton compared to nectaried cotton.

Contact with the frass (excrement plus chewed up/regurgitated plant material) of bollworm larvae results in an intense response by *Microplitis croceipes* females involving a thorough antennal examination of the surrounding substrate (Lewis and Jones, 1971). The most active component from bollworm larval frass is 13-methylhentriacontane, although the females also responded to several related chemicals (Jones *et al.*, 1971). The material on which the larva feeds has been shown to affect the response of *Microplitis croceipes* females to host frass. Frass from bollworm larvae fed on pink-eyed purple hull cowpea cotyledons was significantly more stimulatory than was frass from larvae reared on a modified pinto bean diet (Sauls *et al.*, 1979). Plants also influence the degree of stimulation of extracts of larval frass (Table 7).

Recent studies have clearly shown that learning or conditioning is an important component of the foraging behavior of *Microplitis croceipes* and other parasites (Drost *et al.*, 1986; 1987). For example, exposure of *Microplitis croceipes* females to bollworm larval frass immediately before release of the parasites, resulted in increased rates of parasitization in the greenhouse (27.6 percent for stimulated females versus 0.0 percent for unstimulated females) (Gross *et al.*, 1975). The increase in parasitization due to prerelease exposure to frass was caused by release of an intensive searching behavior and subsequent reduction of the tendency to disperse upon release. In a field study, 16 stimulated females remained to search potted crowder pea plants with only one dispersing, while 21 unstimulated females dispersed, leaving only one to search.

Microplitis croceipes are relatively tolerant of many of the insecticides used in cotton (King *et al.*, 1985c; Powell *et al.*, 1986; Bull *et al.*, 1987; Elzen *et al.*, 1987). Bull

Table 7. Average scored host selection response of *Microplitis croceipes* females to extracts of frass from larvae fed on different plants or cottonseed meal laboratory diet.[1,2]

Food source	Average host selection response[4]
Soybean	1.6a
Cotton	1.0b
Cottonseed meal[3]	0.3c
Corn	0.0c

[1]Means followed by different letters are significantly different ($P<0.05$) as determined by Duncan's multiple-range test.

[2]Data from Nordlund and Sauls (1981).

[3]Burton (1970).

[4]Responses were scored on a three point scale. When a parasite made an extensive examination of a treated spot with her antennae, exhibited considerable excitement, and occasionally probed with her ovipositor (positive response) on the first pass, a score of 3 was given. If a positive response was elicited on the second pass, a score of 2 was given, etc. When a parasite did not respond after three direct passes over the treated spot, a score of 0 was given (Lewis and Jones, 1971). Each replication consisted of the mean score of 10 parasites for each of the test materials.

et al. (1989) reviewed studies of the toxicity of insecticides to adults of this parasite and they identified the following general response pattern: (a) organophosphorus insecticides—highly susceptible to phosphorothionate-type chemicals, relatively tolerant of phosphates; (b) organochlorines—highly susceptible to cyclodienes, relatively tolerant of toxaphene, highly tolerant of DDT; (c) carbamates—tolerant of oxime-type compounds; (d) pyrethroids—highly tolerant. Elzen *et al.* (1989) found that the carbamate methomyl (Lannate®, Nudrin®) caused mortality significantly higher than a mixture of fenvalerate (Pydrin®) and chlordimeform (Galecron®, Fundal®) or the carbamate thiodicarb (Larvin®). The relatively high level of tolerance to certain insecticides which are highly effective against the tobacco budworm may be exploited in a management program that emphasizes conservation of natural enemies.

Cardiochiles nigriceps—Another widely distributed braconid, *Cardiochiles nigriceps*, is found from Washington D. C., south to Florida and west to Kansas, Texas and Mexico (Krombein *et al.*, 1979). It is one of the more important parasites of tobacco budworm larvae (Chamberlin and Tenhet, 1926; Grayson, 1944; Lewis and Brazzel, 1968; Neunzig, 1969; Johnson and Manley, 1983; Roach, 1975; Snow *et al.*, 1966; Smith *et al.*, 1976b). This species can successfully parasitize only tobacco budworm and *Heliothis subflexa* (Lewis *et al.*, 1967) and thus is even more host specific than *Microplitis croceipes*.

Adult *Cardiochiles nigriceps* are robust insects about 3/12ths inch (7 millimeters) long with antennae that are approximately 15/64ths inch (6 millimeters) long (Plate 3-19). The adult insect is black with a red abdomen, most of the hind and lower mid-legs are also red. The antennae are black and the wings are very dark. The ovipositor is short and black and often concealed (Danks *et al.*, 1979). *Cardiochiles nigriceps* is eas-

ily recognized in the field, once the observer is familiar with this insect. The egg and three larval instars are described by Lewis and Vinson (1968).

Cardiochiles nigriceps overwinters in the soil as a prepupa in a cocoon (Danks *et al.*, 1979; Lopez, 1982). Overwintering adults emerge in May in North and South Carolina, April and June in Mississippi, April in Florida, and early June in central Texas (Chamberlin and Tehnet, 1926; Lewis and Brazzel, 1968; Roach, 1975; Danks *et al.*, 1979; Lopez, 1982). There is the potential for overwintering emergence to occur throughout the summer in Central Texas (Lopez, 1982).

Female *Cardiochiles nigriceps* attacked and parasitized all five tobacco budworm larval instars in the field (Lewis and Brazzel, 1966). However, late second and early third instar hosts are preferred (Vinson, 1972).

The rates of parasite development in the various host instars are the same. Small host larvae (first and second instars) continue to grow to the fourth or fifth instar after parasitization while those already in the fourth or fifth instar when parasitized grow very little (Lewis and Brazzel, 1966). The time from oviposition to emergence of a fully developed parasite larva ranged from 11 to 17 days at 80F (26.7C) with most of them completing their development in 13 to 15 days (Lewis and Brazzel, 1966). Developmental times of the egg to larval and prepupal-pupal stages of *Cardiochiles nigriceps* at different constant temperatures are given in Table 8. These results are similar to those reported by Chamberlin and Tenhet (1926). The longevity of adults is temperature dependent (Table 9) and with adults remaining active for approximately two weeks (Vinson *et al.*, 1973).

Table 8. Average duration in days of egg-larval and prepupal-pupal stages of the parasite, *Cardiochiles nigriceps*, at different constant temperatures.[1]

Temperature F (C)	Average number of days	
	Egg-larval stage	Prepupal-pupal stage
62.6 (17.0)[2]	45.1	—
68.0 (20.0)[2]	28.4	—
72.5 (22.5)	19.2	23.0
77.0 (25.0)	14.8	19.3
82.0 (27.8)	11.9	14.8
86.0 (30.0)	10.7	12.8
90.5 (32.5)	9.3	12.2
95.0 (35.0)	9.6	14.8

[1]Data from Butler et al. (1983).

[2]At constant temperatures below 77F (25C), the insects stayed in diapause.

Table 9. Mean longevity in days of males and females of the parasite, *Cardiochiles nigriceps*, at different constant temperatures.[1]

Temperature F(C)	Average number of days	
	Males	Females
68 (20.0	25.6	22.6
73 (22.5)	31.5	30.9
77 (25.0)	19.7	20.2
82 (27.8)	16.3	16.6
86 (30.0)	10.7	9.4
91 (32.5)	15.0	12.9
95 (35.0)	8.0	6.4

[1]Data from Butler et al. (1983).

Cardiochiles nigriceps females will attack both bollworm and tobacco budworm larvae, but no progeny develop in bollworm (Lewis and Brazzel, 1966). *Heliothis subflexa* is also a suitable host while *Heliothis phloxiphaga* Grote and Robinson is unsuitable (Lewis *et al.*, 1967; Lewis and Vinson, 1971). *Cardiochiles nigriceps* eggs or first instar larvae are encapsulated by hemocytes (blood cells in the body cavity of insects) in bollworm larvae (Lewis and Vinson, 1968; Vinson, 1968a). Poison gland material and calyx fluid act synergistically to regulate growth of parasitized tobacco budworm larvae (Guillot and Vinson, 1972).

The host selection behavior of *Cardiochiles nigriceps* females involves responses to a number of semiochemicals. The females are known to be attracted to a number of plants in the field including tobacco (Vinson, 1975), devil's claw [unicorn plant, *Probosidea louisianica* (Mill.) Thellung], and pigeon pea, *Cajanus cajan* L. (personal observation), at least at certain stages in the plants' phenology. Females of *Cardiochiles nigriceps* locate hosts that are hidden from view by responding to a kairomone in the salivary secretion of tobacco budworm larvae which is perceived on contact with the salivary secretion (Vinson and Lewis, 1965; Vinson, 1968b). This kairomone (chemical that elicits a response from the receiving insect) consists of three long-chain hydrocarbons (11-methyl-hentriacontane, 16-methyl-dotriacontane and 13-methyl-hentriacontane) (Vinson *et al.*, 1975). A trail of this material is followed by a female parasite, provided that she is in the proper physiological state. No response is elicited by fecal material or extracts of cuticle, while hemolymph (blood-like circulatory fluid in insects) elicits a negative "flight" response (Vinson and Lewis, 1965).

The response of *Cardiochiles nigriceps* females to the presence of tobacco budworm larval mandibular gland (gland that is on, near or associated with the insect's mouth) kairomone was studied in detail by Strand and Vinson (1982). The female walks in a relatively straight path prior to contacting a kairomone patch (area on a surface with a concentration of kairomone sources). Upon contacting the patch, however, the female stops walking, antennates the patch surface (i.e., searches the patch surface

with its antennae), and then enters the patch. In the patch, the parasite's movement is accelerated and there is a much higher rate of turning than is exhibited prior to entering the patch. When the parasite encounters an edge, it usually will turn sharply back into the patch. Thus, the patch is thoroughly searched for any larvae that might be present.

Cardiochiles nigriceps females also are able to discriminate against previously searched substrates on which first instar larvae had been feeding and against larvae that had previously been parasitized (Vinson, 1972). First instars are small and the female often makes numerous ovipositor thrusts before successfully ovipositing in the host. The ovipositor thrusting may result in deposition of an epideictic pheromone on the substrate allowing discrimination against the patch. The Dufour's gland (a gland associated with the sting or oviposition) has been identified as the source of a hydrocarbon that mediates host discrimination by *Cardiochiles nigriceps* (Vinson and Guillot, 1972; Guillot *et al*., 1974).

Trichogramma spp.—The minute wasps of the genus *Trichogramma* have a worldwide distribution and include over 90 nominal forms (Hung *et al*., 1985) (Plate 3-20). These wasps are parasitic on the eggs of other insects, primarily Lepidoptera, and they are the most extensively used parasite or predator for periodic release programs in the world, with commercial utilization in ten countries (Ridgway and Morrison, 1985). On a worldwide basis, the three most commonly used species of *Trichogramma* are *Trichogramma dendrolimi* Matsumura in China (Li, 1982), *Trichogramma evanescens* Westwood (Sens. Lat.) in Europe (Hassan, 1982; Voegele, 1981; Voronin and Grinberg, 1981) and *Trichogramma pretiosum* Riley in the United States (Ridgway *et al*., 1981).

The biosystematics of these minute wasps are not fully known, at least in part because of their small size. *Trichogramma evanescens* for example was recently divided into two species: *Trichogramma evanescens* and *Trichogramma maidis* Pintureau and Voegele (Pintureau and Voegele, 1980). Thorpe (1984) found 14 biparental and one uniparental species of *Trichogramma* in a 4,842 square feet (450 square meters) plot of weedy vegetation. Some of the more recent taxonomic treatments of the genus are Nagarkatti and Nagaraja (1971, 1977) and Pinto and Oatman (1985).

Trichogramma exiguum Pinto and Platner and *Trichogramma pretiosum* were the two most common native species in Portland, Arkansas; Clinton, North Carolina (Hung *et al*. 1985) and in Central Texas (López *et al*., 1982). *Trichogramma exiguum* has a yellow head marked with transverse lines above the antennal sockets. The thorax and pronotum have brown spots on each side. The brown coloration is more extensive in the male. The exact range of *Trichogramma exiguum* is unknown, but it is found in Alabama, Arkansas, Missouri, Texas and probably as far south as Peru (Pinto *et al*., 1978; López *et al*., 1982; Hung *et al*. 1985). *Trichogramma pretiosum* has a yellow head and thorax. The thorax is suffused with brown laterally (i.e., a brown coloring with streaking on the sides of the thorax). The legs are light yellow, marked with dark brown on the dorsum (the back or top side) of the femora (third leg segment

located between the trochanter and the tibia) and tarsi (the part of the leg beyond the tibia, consisting of one or more segments). The abdomen is yellow brown, darker medially at the posterior. This species is found throughout southern Canada and the United States, except the most southern and southwestern areas, and south to Colombia, South America (Pinto *et al.*, 1978; Krombein *et al.*, 1979). Both of these species are found in campestral (fields or open country) habitats.

The first appearance of *Trichogramma pretiosum* in the spring corresponds approximately with the first general occurrence of bollworm eggs on corn (Quaintance and Brues, 1905). In a study conducted in Central Texas, Lopez *et al.* (1982) found *Trichogramma* parasitizing corn earworm or bollworm eggs in corn from the middle of May until the corn matured. The species involved were *Trichogramma exiguum* (69.6 percent), *Trichogramma pretiosum* (20.9 percent), *Trichogramma maltbyi* Nagaraja and Nagarkatti (6.1 percent) and *Trichogramma minutum* Riley (3.4 percent). In cotton, *Trichogramma pretiosum* was the most common species (78.3 percent) and it was active through the middle of September. In regrowth grain sorghum in September and October, *Trichogramma exiguum* was again dominant (71.7 percent). The study shows that *Trichogramma exiguum* and *Trichogramma pretiosum* are active throughout the growing season. The generation time for *Trichogramma pretiosum* is eleven days in May, decreasing to eight days in July and August and lengthening to eleven days by the beginning of October (Quaitance and Brues, 1905). Lepidopterous eggs parasitized by *Trichogramma* turn dusky black in color a few days after being parasitized and observation of an accummulation of black eggs on cotton plants in the field indicates a high level of parasitization by these parasites.

There is considerable difference in the longevity estimates for *Trichogramma* in the literature Quaintance and Brues (1905) found that *Trichogramma pretiosum* adults live at most four days witn an average life span of one and a half days. Orphanides and Gonzalez (1971) found that mean longevity varied from 16.8 days to 20.6 days with varying host densities at 77F (25C), 80 percent relative humidity and a 13 hour photophase. Nordlund et al. (1976) found that the average adult longevity of *Trichogramma pretiosum* females reared on bollworm/tobacco budworm eggs at 78.8F (26C) and 70 percent relative humidity and provided honey water, was 10.6 days for females that were not in contact with moth scale extract and 12.2 days for females in contact with this material. Some of the females lived as long as 24 days. Keller and Lewis (1985) found that the longevity of *Trichogramma pretiosum,* which had been reared on *Sitotroga cerealella* (Olivier) eggs, conditioned for release (Bouse and Morrison 1985) and held at ambient conditions in the field, varied between 0.9 and 3.8 days.

Trichogramma pretiosum and *Trichogramma exiguum* overwinter in the immature stages inside the host egg. Adults emerge during warm winter periods and are active at relatively low temperatures. Apparently, diapause is not involved and the decrease in developmental rate is primarily due to the lower winter temperatures (Lopez and Morrison, 1980; Keller, 1986). Keller (1986) reported that prolonged adult longevity of *Trichogramma exiguum* due to low temperatures during the winter also contributes

to the overwintering of that species. Mild fall temperatures may have a considerable impact on overwintering populations because parasitization of host eggs occurs relatively late in the fall when host eggs are scarce.

Trichogramma pretiosum was the only parasite reared from bollworm eggs collected from sweet corn in southern California during a three year study (1963 to 1965) (Oatman, 1966). An average of 2.1 *Trichogramma* emerged per bollworm egg. Parasitization rates ranged from 0 to 100 percent. Parasitization was generally higher on sweet corn maturing during the middle of the season (August) than on plantings that matured earlier or later. *Trichogramma pretiosum* can be used to control cabbage looper, and tobacco hornworm, Manduca sexta (L.), in California tomatoes (Oatman and Platner, 1971).

Semiochemicals play important roles in the host selection behavior of *Trichogramma. Trichogramma evanescens* responds to kairomones left by adult moths (Laing, 1937). Chemicals in bollworm moth scales can be used to increase the rate of parasitization by *Trichogramma evanescens* (Jones et al., 1973; Lewis *et al.*, 1975). Bollworm moth scales stimulate an intensive host location behavior in *Trichogramma pretiosum* and treatment pattern is important (Lewis *et al.*, 1979, Beevers et al., 1981).

Semiochemicals from plants are also important. Altieri *et al.* (1981) found that water extracts of *Amaranthus* spp. (pigweeds) and corn significantly increased parasitization of bollworm by naturally-occurring *Trichogramma* spp. and released *Trichogramma pretiosum* in soybean fields. *Trichogramma* spp. parasitized bollworm eggs at significantly higher rates on tomato than on corn (Nordlund et al., 1984). Tomato contains a synomone(s) [a substance produced or acquired by an organism that when it contacts an individual of another species in the natural context, evokes in the receiver a behavioral or physiological reaction that is adaptively favorable to both emitter and receiver (Nordlund and Lewis, 1976)] that stimulates host habitat location behavior in *Trichogramma pretiosum* (Nordlund et al., 1985a, b). Compounds in the sex pheromone used by bollworm females also stimulate host selection behavior by *Trichogramma pretiosum* (Lews et al., 1982). Once a host egg is located, chemicals in the accessory gland secretaion, used by the female moths to attach eggs to the substrate, are important in host recognition (Nordlund et al., 1987).

Host plant resistance characters influence *Trichogramma pretiosum* parasitism of bollworm eggs on cotton (Treacy et al., 1985, 1987 a, b). Fewer eggs were parasitized on pilose cotton phenotypes compared to smoothleaf and hirsute cottons due to inhibition of movement of *Trichogramma pretiosum* females over leaf surfaces by the higher density of cotton leaf trichomes (hairs). The nectariless character reduces parasitism of bollworm/tobacco budworm eggs when compared to nectaried cotton by both *Trichogramma pretiosum* and naturally occurring *Trichogramma* spp.

Adult *Trichogramma* are generally highly susceptible to broad-spectrum insecticides (Jacobs et al., 1984; Bull and Coleman, 1985). Thus, their use in integrated pest management and periodic release programs will likely be limited to systems where insecticides are not used or are used only sparingly.

There has been considerable research effort expended to bring about practical use of *Trichogramma* in periodic release programs. To date the results have been mixed (Ridgway and Morrison, 1985). In the United States, emphasis has been directed toward use of *Trichogramma pretiosum* to control bollworm/tobacco budworm on cotton, a very complicated system. Ridgway and Morrison (1985) identified several research areas that, if addressed, could likely remove technical barriers to the practical use of *Trichogramma:*

- Selection of the most effective species or strain;
- Reduction of loss of efficiency resulting from dispersal;
- Improvement of production and release efficiency;
- Increased knowledge of the relationships between the numbers of *Trichogramma* and pests and changes in yield;
- Improved prediction and survey method for pests and naturally occurring predators and parasites; and,
- Design and implementation of insect management systems that will eliminate or substantially reduce insecticide interference.

FLIES

Archytas marmoratus—*Archytas marmoratus* is a large [about 1/2 inch long (12 to 13 milimeters)] tachinid parasite which is found throughout the southern United States to Peru and in the West Indies (Sabrosky, 1955; Sabrosky and Arnaud, 1965; Ashley, 1979) (Plates 3-21 and 3-22). It is a larviparous (deposits live maggots rather than eggs) larval-pupal parasite can attack a number of lepidopterous hosts (Table 10). This species is generally more abundant late in the season, though it was collected every month of the year, except February, near Brownsville, Texas (Vickery, 1929). Archytas marmoratus is a major parasite of bollworm/tobacco budworm and has been reared

Table 10. Hosts of the parasite, *Archytas marmoratus*.

Host	Source/reference
Black cutworm	Thompson (1951)
Hyblaea puera Cramer	Thompson (1951)
Mocis repanda F.	Thompson (1951)
Mocis latipes	Scaramuzza (1946)
Leucania latuiscula	Vickery (1926)
Fall armyworm	Vickery (1926)
Spodoptera latifascia	Patton (1958)
Armyworm	Vickery (1926)
Bollworm	Hughes (1975)
Tobacco budworm	Hughes (1975)
Heliophila spp.	Vickery (1915)
Laphygma spp.	James (1953)

from bollworm/tobacco budworm larvae collected from alfalfa, corn, cotton, sugarcane and tobacco (Quaintance and Brues, 1905; Vickery, 1926; Bibby, 1942; Bottrell and Arnold, 1968; Bottrell et al., 1968; Neunzig, 1969; Miller, 1971; Shepard and Sterling, 1972a). Shepard and Sterling (1972a) found that 43 percent of the parasites recovered from bollworm/tobacco budworm spp. larvae collected from cotton growing near Angleton, Texas were *Archytas marmoratus*. It was the only parasite found attacking bollworm larvae in whorl and early tassel-stage corn growing near Tifton, Georgia (Gross et al., 1976).

Archytas marmoratus females larviposit their bluish green maggots on foliage rather than directly on the host larvae (Hughes, 1975). Larviposition is stimulated by a kairomone from the host. Nettles and Burks (1975) found that a protein, with a molecular weight of 30,000 ± 5,000, present in tobacco budworm larval frass, hemolymph and whole body extract, stimulates larviposition. The maggots then attach themselves to hosts that crawl by and enter the host integument; they kill the host after it pupates (Hughes, 1975).

During larviposition, the free-living first instar maggots are anchored individually to the substrate by the chorion, which is compressed and cup-like, enveloping the caudal (rear) end of the maggot. The maggots lay horizontally on the substrate until they are disturbed and then assume a vertical position, and wave about in a circular motion. Hughes (1975) found that maggots, larviposited on young corn plants in rearing rooms (16 hours photophase, 55 percent relative humiidity) lived for 5 to 6 days at 80.6F (27C) and 13 to 14 days at 69.8F (21C). The maggots attach to host larvae and normally penetrate the host's integument within 12 hours. While the host's integument is being cast off during molts, the maggots leave the old integument, move to the new integument, and penetrate. This press continues until pupation, which occurs in an underground tunnel excavatged by the host larva. During pupation the maggots move from the old integument over the surface of the pupae and enter under the posterior wing pad margins. After penetration, the parasite begins development, goes through three larval instars and then pupates within the host's remains. Generally, only one puparium is formed per host. Developmental times at 80.6F, are 22 to 46 hours for first instar, 2 to 4 days for second instar and third instar lasts for 3 to 4 days. At 69.8F, the time between host pupation and parasite pupation is 8 to 10 days (Hughes 1975). Because the pest is killed in the pupal stage, parasitized larvae cause as much damage on cotton as unparasitized larvae. Thus, this parasite might be useful in a long-term population reduction program, but not for direct therapeutic control.

Hughes (1975) reared *Archytas marmoratus* from fourth to sixth instar bollworm and third to sixth instar tobacco budworm larvae collected from tobacco near Clayton, North Carolina. He found that maggots would readily attach to second to fifth instar hosts.

Archytas marmoratus are relatively long-lived insects with females living longer than males. Hughes (1975) reports that at 69.8F, females lived an average of 72.8 days while at 80.6F, they lived an average of 51.2 days; males lived 19.0 and 9.8 days at these respective temperatures. Adults emerge during warm periods in the winter and it

appears that these adults are able to survive the winter (López, unpublished data). No diapause apparently is involved in the overwintering of this parasite at least when parasitizing bollworm/tobacco budworm in the fall for overwintering. The females exhibited a prelarvipositional period of 14.6 and 10.9 days and a larviposition period of 36.7 and 38.0 days at 69.8F and 80.6F, respectively. Fecundity was also influenced by temperature, with a mean of 1845 and 2828 maggots produced per female at 69.8F and 80.6F, respectively. Gross and Johnson (1985) report on procedures for large scale rearing of *Archytas marmoratus.*

Eucelatoria bryani—One of the most common tachinid parasites of bollworm/tobacco budworm larvae is *Eucelatoria bryani,* (Jackson *et al.,* 1969; Bryan *et al.,* 1970; Werner and Butler, 1979). It ranges from Mississippi, north to Missouri, west through Kansas to Arizona and south through Mexico to Nicaragua and El Salvador (Sabrosky, 1981). It also has been introduced into India and Trinidad for control of *Helicoverpa/Heliothis* (Sabrosky, 1981). This tachinid is a small [5/32nds to 5/16ths inch long (4 to 8 millimeters)], active, grayish-black fly with a reddish tinge at the tip of its abdomen (Plate 3-23). This parasite also can attack cabbage looper larvae; however, for all practical purposes it is limited to bollworm/tobacco budworm larvae. It has a much more narrow host range than does the closely related species, *Eucelatoria armigera* (Coquillett), found in California (Bryan *et al.,* 1970). *Eucelatoria* sp. (probably Eucelatoria bryani) was the most common tachinid parasite of bollworm/tobacco budworm trapped by Werner and Butler (1979) in cotton near Phoenix, Arizona. It was most common in late June and early July.

Most published studies on the biology of *Eucelatoria bryani* have used fourth and fifth instar bollworm/tobacco budworm larvae. However, *Eucelatoria bryani* can successfully parasitize second through fifth instar and prepupal bollworm larvae in the laboratory (Martin et al., 1989). These findings mean that this parasite may be a more prising biological control agent than was previously though because it can attack a broader range of larval stages.

Eucelatoria bryani has three larval instars: the first instar stage lasts for about 28 hours; the second for about 32 hours; and the thrid for about 36 hours at 84.2F (29C) (Ziser and Nettles, 1978). The larvae then emerge from the host, form puparia (hardened cases in which the pupa is formed) and pupate. Emergence from the host in the field occurs from the fully developed host larva that has dropped from the plant and excavated a tunnel underground in preparation for pupation. Emergence from the host and formation of a puparium occurs: (a) when all available food is consumed, (b) when the maggot has reached maximum size; or (c) if the humidity of the maggot's environment decreases (Ziser and Nettles, 1978). As with insects in general, temperature has a major influence on the time required for development and on the longevity of this parasite (Tables 11 and 12). *Eucelatoria bryani* is similar to Archytas marmoratus in that the adults emerge during warm periods in the winter and the adults are apparently able to survive the winter (López, unpublished data).

Table 11. Average length of developmental stages in days of the parasite, *Eucelatoria bryani*[1], in tobacco budworm at different temperatures[2].

Rearing Temperature F (C)	Average number of days Larval	Pupal	Average total number of days to complete development
59 (15)	14.2	32.4	46.6
68 (20)	6.7	14.9	21.6
77 (25)	4.7	8.9	13.6
86 (30)	3.8	7.3	11.1

[1]*Eucelatoria* sp. from Bryan et al. (1970) was later identified as *Eucelatoria bryani* by Sabrosky (1981).
[2]Data from Bryan et al. (1970).

Table 12. Average longevity in days of males and females of the parasite, *Eucelatoria bryani*, under different constant temperature regimes.[1]

Temperature F (C)	Average longevity in days Male	Female
68 (20.0)	52.5	61.8
77 (25.0)	34.1	44.1
86 (30.0)	21.1	31.0
90 (32.2)	14.8	22.9
95 (35.0)	11.1	17.9

[1]Data from Bryan *et al.* (1972).

The prelarviposition period of *Eucelatoria bryani* females ranges from five to nine days and the larviposition period ranges from one to 29 days, depending on temperature. Larviposition by *Eucelatoria bryani* peaks during the first 10 days of the female's larviposition period, when the insects were held at 86F (30C). *Eucelatoria bryani* parasitized more larvae, in the laboratory at 77 to 86F (25 to 30C) than at lower (68F) or higher (90F) temperatures (Bryan et al., 1972).

The host selection behavior of *Eucelatoria bryani* females involves responses to a number of semiochemicals. They are attractedto a variety of plants by volatile semiochemicals. Nettles (1980) found okra leaves to be more attractive than cotton leaves. Martin et al. (1990) found that several other plants/plant parts, including corn silks, pigeon pea flowers, tobacco flowers, tomato leaves and sorghum panicles are attractive to females, while devil's claw (unicorn plant) leaves and cotton leaves are not. A kairomone from the cuticles of tobacco budworm larvae, which is extractable in chloroform: methanol (1:1), induces larviposition behavior in *Eucelatoria bryani* females (Burks and Nettles, 1978). The hosts's diet affects the attractiveness of the host in an olfactometer (Nettles, 1980). The flies do not respond to either southern armyworm, *Spodoptera eridania* (Cramer), or saltmarsh caterpillar, *Estigmene acrea* (Drury).

Nettles (1982) reported that flies aggregated on filterpaper that had been treated with various materials from tobacco budworms, including fresh frass, hemolymph, vomit, and a hexane extract of frass.

Eucelatoria bryani females stand on the host larva to larviposit, and in a single very rapid motion, use an abdominal barb to rip the host's integument and the oviscapt to inject maggots into the host. Jackson *et al.* (1969) reported finding as many as 20 maggots in a single host immediately after parasitization.

SUMMARY

By improving our understanding of the biology, ecology, and impact of predators and parasites, it has been possible to develop models capable of forecasting the economic impact of pests and their natural enemies. Though there has been considerable progress, there is a great need for expanding and validating models under practical field conditions. This should lead to systems in which it is possible to accurately estimate the true costs and benefits of all pest management actions.

Claims of the importance of various groups or species of natural enemies in checking the abundance of plant-eating arthropods of cotton are generally lacking conclusive evidence. For example, there is a shortage of life table information that identifies all mortality throughout the total generation of the host and which identifies the precise cause of mortality of each individual. Thus, it is virtually impossible to make claims of importance based on evidence of irreplaceable mortality. Until life tables are completed for each key arthropod pest of cotton, we will continue to be forced to make assumptions based on fragmented studies in the literature. Complete life tables, similar to those of Sturm *et al.* (1989) for boll weevils, are needed from untreated cotton fields in several locations in the Cotton Belt over several years. Without this information, it will be impossible to develop highly accurate models using the total complex of predators, parasites and pathogens designed to forecast insect/mite pest economics and to understand the complex linkages between the plant, insect/mite pests, and their natural enemies. In this chapter, we present evidence and summarize the importance of the species of those natural enemies which presently are considered to be significant; however, future studies as well as changes in the agroecosystem brought about by man, by selection or that result from changes in the law will undoubtedly modify our choices.

This review of how different factors influence the biology, ecology and efficacy of selected natural enemies of arthropod pests of cotton identifies factors that may be manipulated to maintain or increase the densities of the natural enemy complex or their suppressive effects on pest populations in cotton fields. These manipulations involve the prision of environmental requisites, use of semiochemicals and modification of production or cropping practices. In the short term, the most immediate opportunities for maximum utilization of the natural enemy complex are probably in the modification of production or cropping practices. In the longer term, we must continue to explore the potential of manipulations which require the provision of environmental

requisites and the use of semiochemicals. Pressure from society will continue to increase for a more biorational approach to pest management in cotton. A major basis for the approach will likely be the cultural and biological control of cotton pests. Maximum utilization of natural enemies will play a major role in cotton pest management programs that are compatible with sustainable agriculture ideals.

Chapter 3

APPENDIX

The color plates that follow in this appendix are photographs of some of the predators and parasites that are discussed in this chapter. Some of these photographs depict a predator feeding on a cotton insect or mite pest; other photographs depict a parasite in the act of parasitizing a cotton insect pest.

Plate 3-1. Cotton fleahopper, *Pseudatomoscelis seriatus,* nymph feeding on an egg of the bollworm, *Helicoverpa zea.*

Plate 3-2. Adult *Geocoris* (bigeyed bug) feeding on an adult of the cotton fleahopper.

Plate 3-3. Nymph of *Geocoris punctipes* feeding on eggs of the bollworm.

Plate 3-4. Adult of *Chrysoperla rufilabris.*

Plate 3-5. Narrow black or dark-red band from eye to mouth over the genae (lateral part of the head) on the adult of *Chrysoperla carnea,* common green lacewing.

Plate 3-6. Larva of common green lacewing, *Chrysoperla carnea,* feeding on a bollworm egg.

Plate 3-7. Larva of *Chrysoperla rufilabris* feeding on a bollworm larva.

Plate 3-8. Eggs of *Chrysoperla* on a cotton leaf. Eggs of common green lacewing, *Chrysoperla carnea* and *Chrysoperla rufilabris* (no common name) are oviposited singly and not in groups as shown.

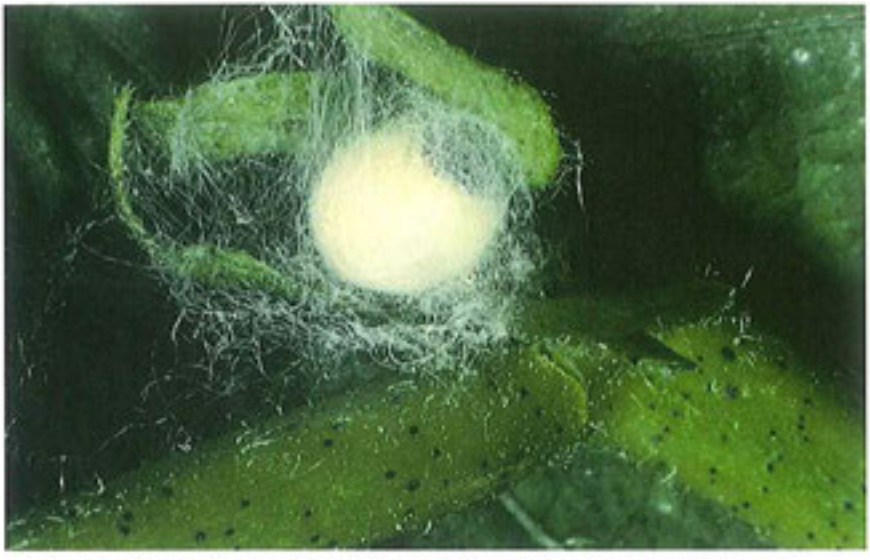


Plate 3-9. Cocoon of common green lacewing, *Chrysoperla carnea* on a cotton leaf.

Plate 3-10. Adult of minute pirate bug, *Orius tristicolor,* feeding on a boll-worm larva.

Plate 3-11. Nymph of insidious flower bug, *Orius insidiosus.*

Plate 3-12. Red imported fire ant, *Solenopsis invicta,* feeding on a boll-worm egg.

Plate 3-13. Striped lynx spider, *Oxyopes salticus,* feeding on a cotton fleahopper.

Plate 3-14. Winter spider, *Cheiracanthium inclusum,* feeding on a bollworm larva.

Plate 3-15. Ridge-faced crab spider, *Misumenoides formosipes* (Walckenaer), feeding on a cotton fleahopper.

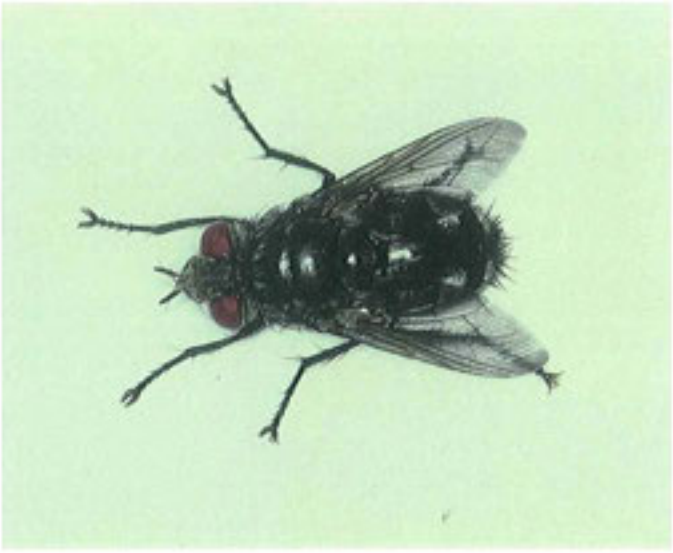
Plate 3-16. Celer crab spider, *Misumenops celer,* feeding on a cotton flea-hopper.

Plate 3-17. Black and white jumping spider, *Phidippus audax,* feeding on an adult boll weevil.

Plate 3-18. *Microplitis croceipes* parasitizing a bollworm larva. (Photo courtesy of the USDA, ARS Information Office, Beltsville, MD.)

Plate 3-19. *Cardiochiles nigriceps* feeding at a nectary on a cotton leaf. (Photo courtesy of S. B. Vinson, Department of Entomology, Texas A&M University, College Station, TX.)

Plate 3-20. *Trichogramma pretiosum* parasitizing a bollworm egg. (Photo by Jack Kelly Clark, courtesy of the University of California Statewide IPM Project, Davis, CA.)



Plates 3-21 and 3-22. Adult of the parasite *Archytas marmoratus.* (Photos courtesy of Harry R. Gross and James E. Carpenter, USDA, ARS, Insect Biology and Population Management Laboratory, Tifton, GA.)

Plate 3-23. *Eucelatoria bryani* parasitizing a bollworm larva. (Photo courtesy of William C. Nettles, Jr., USDA, ARS, Subtropical Agricultural Research Laboratory, Weslaco, TX.)

Chapter 4

SHORT- AND LONG-RANGE MOVEMENT OF INSECTS AND MITES

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INTRODUCTION

Agroecosystems of annual crops such as cotton provide a transient reproductive habitat for many economically damaging insects and other pests. The cotton field is a dynamic habitat (Cross, 1983) and derives most of its arthropod populations from surrounding natural or cultivated plants. The role of both managed and unmanaged hosts in producing pest and beneficial species of arthropods invading cotton fields has long been acknowledged and will be addressed in discussions of specific insects in this

chapter. Mobility is a major factor in the population dynamics of organisms using cotton as a temporary reproductive habitat. Although the role of long distance movement on population dynamics in agricultural systems is not as clearly defined, or as well understood as the localized movement between and within fields, increasing circumstantial evidence indicates that many cotton pests, especially Lepidoptera, are capable of long distance movement.

Ridgway (1986) suggested that the choice of control strategies for insects should be based on specific criteria, including the target insect's dispersal characteristics. Ridgway further stated that understanding the quantitative population ecology of the bollworm, *Helicoverpa zea* (Boddie) and the tobacco budworm, *Heliothis virescens* (F.) (appropriate for some other insects as well) is critical for guiding future research in control tactics. Understanding migratory and dispersal capabilities of highly mobile insects is pivotal in determining the possible success or failure of many control strategies.

BOLLWORM/TOBACCO BUDWORM

The *Helicoverpa/Heliothis* genera have a worldwide distribution and their pest status is attributed, in part, to their mobility (Farrow and Daly, 1987). Due to this mobility as well as a highly polyphagous (ability to feed on many kinds of food [plants]) behavior, *Helicoverpa/Heliothis* are well adapted to exploitation of unstable habitats such as annual crops. These behavioral traits facilitate the rapid deployment of populations between fields as well as between crops and naturally occurring host plants.

The classification of movements observed in *Helicoverpa/Heliothis* adult populations has been difficult (Fitt, 1989), and various terminologies to describe their mobility abound. Farrow and Daly (1987) defined *Helicoverpa/Heliothis* movement as short-range <.6 mile (<1 kilometer), long-range 0.6 to 6 miles (1 to 10 kilometers) and migratory 6 to 300 miles (10 to 500 kilometers). However, they recognized that distinctions between these categories were rather ill-defined, and that the scale of movement depended on atmospheric conditions, distribution of suitable habitats and moth behavior.

SHORT-RANGE MOVEMENT

Short-range movement of *Helicoverpa/Heliothis* as defined by Farrow and Daly (1987) includes much of the movement involved in individual survival (feeding and seeking daytime refuge), and attraction to host plant concentrations for oviposition and mate-seeking. Within a localized adult population where suitable host plants abound, this type of movement begins near sundown and may continue at various levels of intensity throughout the night. Short-range movement usually occurs within or immediately above the crop canopy with the insects oriented up- or cross-wind. Orientation during short-range movement is probably due to responses to chemical stimuli (Lingren and Wolf, 1982) produced by the plant or by sexually receptive females (pheromonal stimuli). Various behaviors associated with this type of movement were described by Raulston *et al.* (1975); Raulston *et al.* (1976); Lingren *et al.* (1977); Lingren *et al.* (1979); and Lingren and Wolf (1982).

Agriculturally important hosts such as cotton may provide an ideal (although temporary) habitat for colonizing adults by providing them both shelter, food and attractive reproductive sites (for mating and oviposition). However, movement between fields and crops occurs resulting in a constant redistribution of the adults (Haggis, 1982; Joyce, 1982; Stinner *et al.*, 1982).

LONG-RANGE MOVEMENT

Long-range movement by *Helicoverpa/Heliothis* as defined by Farrow and Daly (1987) resulting in a displacement of a few kilometers, in many instances can still be considered appetitive or trivial since it may involve the seeking of mates, feeding sources and refuge. However, long-range movement which can occur within a few minutes may also involve the searching for more attractive host sites. Orientation and displacement associated with this movement is usually downwind and occurs within the first few tens of meters above the crop canopy. Observations using high intensity light beams and night vision goggles indicate that such movement begins at dusk and that the adults ascend to at least a height of about 100 yards (92 meters), which was the range limit of equipment used.

Long-range movement of corn earworm (same as bollworm) may also result in the redistribution of adults between habitats within an area. As the more attractive hosts (such as corn) mature, adults begin to colonize crops such as tomatoes, cotton and soybean which are considered to be less attractive hosts (Quaintance and Brues, 1905; Garman and Jewett, 1914; Pepper, 1943; Stinner *et al.*, 1982; Raulston *et al.*, 1986a; Raulston *et al.*, 1986b). Snow *et al.* (1969) reported that radiolabled bollworms, which developed in a centrally located corn field on the island of St. Croix, dispersed and concentrated around areas with attractive host plants.

Haggis (1982) analyzed the distribution of *Helicoverpa armigera* (Hübner) eggs over a 3200 square mile (8300 square kilometers) area of the Sudan Gezira and found that within each two to three day observation period, two or more significantly different levels of infestation occurred, each covering areas up to several thousand square miles with continuously changing boundaries. Haggis suggested that the major cause for the fluctuating population boundaries was a constant redistribution of adults with changing synoptic (over a broad area) and mesoscale (localized) weather patterns.

MIGRATORY MOVEMENT

Migratory movement exceeding 60 miles (100 kilometers), provides another mechanism for *Helicoverpa/Heliothis* to exploit ephemeral (temporary or short- term) habitats. This type of movement, in many instances, appears to be facultative in nature (Hackett and Gatehouse, 1982) and may occur in response to a decaying habitat. Migratory movement typically begins at dusk (Lingren and Wolf, 1982; Drake, 1984, 1985; Wolf *et al.*, 1986) with the adults rapidly ascending to an altitude of up to 1000 yards (914 meters). Radar observations (Drake, 1985; Wolf, 1986) indicate that migrants frequently form layers near or just above the maximum wind velocity associated with nocturnal low-level jets (airstreams). Wind velocity in these airstreams fre-

quently exceed 30-36 miles per hour (50-60 kilometers per hour) and can transport migrating moths over 180 miles (300 kilometers) during a five-hour flight. Drake and Farrow (1988) presented an excellent review on the atmospheric structures that provide transport mechanisms facilitating migratory movement.

Evidence that *Helicoverpa/Heliothis* undergo migratory movement includes the fact that they annually invade areas beyond their overwintering range. Also, they have been detected in areas where they do not breed and marked individuals have been captured many miles (kilometers) from their release sites. The overwintering range of the bollworm has been reported to extend northward to about 40 degrees north latitude (Snow and Copeland, 1971). However, Hardwick (1965) reported that in some years the bollworm is found up to 50 degrees north latitude. Hardwick (1965) also indicated that the overwintering range of *Helicoverpa armigera* is roughly bordered by 40 degrees north and south latitudes; however, this species has been reported as far north as Narva, Estonia, at about 59 degrees north. French and Hurst (1969) documented the arrival of *Helicoverpa armigera* in the British Isles at about 51 degrees north latitude in July 1968. Through correlation with meteorological events, they were able to backtrack the insects to their probable origin in northwestern Spain or north Africa, a distance of 480 to 960 miles (800 to 1600 kilometers). Callahan *et al.* (1972) captured bollworm moths in light traps mounted on top of a 318 yard (290 meter) television tower located near Pelham, Georgia. They concluded that these moths were in migratory flight. Sparks *et al.* (1975) captured bollworm moths in light traps located on unmanned oil rigs in the Gulf of Mexico 96 miles (160 kilometers) south of Jeanerette, Louisiana and determined that these insects were transported to sea by frontal movements. Haile *et al.* (1975) reported movement of released tobacco budworm and bollworm moths from St. Croix to the islands of St. Thomas and Veiques, a distance of 36.6 and 43.2 miles (61 and 67 kilometers) respectively. Released laboratory reared bollworm moths near Tifton, Georgia dispersed up to 15 miles (25 kilometers) in one night and up to 43.2 miles (72 kilometers) in one to four nights (Sparks, 1972). In a similar study near Brownsville, Texas, Hendricks *et al.* (1973) recaptured tobacco budworm moths up to 67.2 miles (112 kilometers) downwind from the site of their release. Raulston *et al.* (1982) captured feral (wild) tobacco budworm moths in the Lower Rio Grande Valley and released them near San Fernando Tamaulipas, Mexico. Subsequently, some of these moths were recaptured in the Lower Rio Grande Valley, after they had flown a distance of 96 miles (160 kilometers) from San Fernando.

Asynchrony (lack of synchrony) between emergence of moths from local populations and the occurrence of initial trap captures also has provided evidence of migratory movement (Stadlebacher and Pfrimmer, 1972; Raulston, 1979; Hartstack *et al.*, 1982). Furthermore Hendrix *et al.* (1987) collected bollworm moths in Arkansas with pollens that the moths carried at least 450 miles (750 kilometers).

IMPLICATIONS OF *HELICOVERPA/HELIOTHIS* MOBILITY

Since the advent of efficient pesticides, control strategies for *Helicoverpa/ Heliothis* have relied on field-by-field defensive measures to suppress larval populations. However, the indiscriminate use of pesticides, which were often applied on an empir-

ically scheduled basis, is no longer an environmentally or economically viable pest management option. The constant redistribution of adult populations through short- and long-range nocturnal movements requires that susceptible crops such as cotton be constantly monitored for the presence of egg/larval populations to properly time control measures, if needed. Furthermore, the influence of movement in developing *Helicoverpa/Heliothis* control strategies that do not rely completely upon pesticides, must be addressed (Fitt, 1989). The high mobility characteristics of *Helicoverpa/Heliothis* may often negate the possibility of adequately predicting egg and larval populations based on the immediate past history of individual fields since adults may be derived from adjacent crops and wild host plants as well as from other regions. The problems that arise as a result of adult movement is compounded in areas with diverse cropping systems where a succession of cropped host plants are available to the insect.

The mobility of *Helicoverpa/Heliothis* adults provides both opportunities and constraints for developing population suppression technology. Moth mobility allows the female to disperse her eggs over relatively large areas on a variety of hosts. This requires the use of large volumes of pesticides (with an array of negative side effects) over large areas to facilitate larval control in susceptible crops. Moth mobility also is a major constraint for developing, or even adequately researching suppression technology using pheromones as mating suppressants. Movement of previously mated females into pheromone-treated areas can effectively mask any treatment effects unless plots are large enough to reduce the possibility of immigration. The ability of *Helicoverpa/Heliothis* moths to rapidly disperse (Haggis, 1982) may also reduce the effects of natural enemies in controlling *Helicoverpa/Heliothis* populations. If inadequate populations of natural enemies are present or if their dispersal is not at the same rate as the pest into colonization areas, control will be inadequate. For example movement of beneficial insects can be affected by the occurrence of alternate food sources within a field or area. Thus, if a large biomass of relatively sessile (immobile) prey, such as aphids, were available within a field from which moths were dispersing, a concurrent dispersal of beneficial insects may not occur.

Techniques for suppressing moth populations that reduce the impact or take advantage of their mobility have been deployed or suggested. In Arkansas, the establishment of management communities resulted in a reduced number of pesticide applications being applied for control of the bollworm (Phillips, 1978). The use of management communities enables synchronous pesticide applications over a large enough area 30+ square miles (80+ square kilometers) to negate the effects of short-distance movement by moths. Another technique that may take advantage of moth mobility is the manipulation of the adult population through the use of trap crops (see Fitt 1989, for review) that provide attractive feeding or reproductive sites. Lingren *et al.* (1982), Lingren and Wolf (1982) and Lingren *et al.* (1988), suggested that a thorough understanding of the nocturnal (nighttime) behavior of moths will facilitate the development of efficient adult control technology.

The agricultural community must address the entire ecosystem within any given region to adequately determine the how, when, and where of pest population deriva-

tion. Then based on this knowledge, areawide suppression technologies as proposed by Knipling (1979) and Johnson *et al.*(1986) may be applied with success.

PINK BOLLWORM

The pink bollworm, *Pectinophora gossypiella* (Saunders) is recognized as one of the most important economic pests of cotton throughout the world. It was described in 1843 from specimens damaging cotton in India (Noble, 1969). From India the pink bollworm apparently reached Egypt in infested cottonseed shipped in 1906 or 1907, and subsequently reached the western hemisphere in infested cottonseed shipped from Egypt to Mexico between 1911 and 1913 (White, 1960). The insect was first detected in the United States in cottonseed shipped in 1916 from Mexico to Texas oil mills. Initial United States infestation was apparently eradicated in Texas using cotton-free zones and extensive cultural measures. Subsequent infestations in Louisiana, Arizona, Georgia and Florida were also eliminated (infestation still exists in wild cotton in Southern Florida) (Anonymous, 1977).

Reinfestation of the Lower Rio Grande Valley of Texas by the pink bollworm in 1936 was suspected to have occurred from moth migration from Mexico. By the mid-1950s, all the cotton growing areas in Texas, New Mexico and Oklahoma, as well as large areas of Arizona, Arkansas, and Louisana were infested. By 1965, the pink bollworm had infested all of the cotton-growing areas in Arizona and for the first time had been reported in southern California. Thus, by 1967, most cotton west of Louisiana and Arkansas except in California's San Joaquin Valley was infested (Spears, 1968).

The role of moth flight in the spread and establishment of pink bollworm infestations became of interest after unexplained reinfestations occurred in cotton in the Big Bend area of Texas. These reinfestations followed two years of cotton-free zone restrictions as well as other eradication measures that had been successful in other areas (Coad, 1929; McDonald and Loftin, 1935). Infestations also were detected in other valleys along the Rio Grande and Pecos Rivers in Texas and New Mexico, and in small isolated cotton fields located 24 to 48 miles (40 to 80 kilometers) from known infestations. Ohlendorf (1926) demonstrated that cotton fields isolated from infested cotton by 1 to 39 miles (1.6 to 65 kilometers) became heavily infested with pink bollworm by late-July to mid-October in Mexico, suggesting late-season moth flight from infested to uninfested cotton. Similarly, Fenton (1929), McDonald and Loftin (1935), and Fenton and Owen (1953) reported that cotton plots isolated by 3.6 to 72 miles (6 to 120 kilometers) from infested cotton in Texas unexpectedly became infested. Of the 90 plots investigated over a six-year study period, 18 became infested from late-September to November. Generally, rapid increases in field infestations occurred shortly after the number of pink bollworm moths captured in sticky traps increased. These authors observed that the spread and intensity of pink bollworm infestations in the southwestern part of the United States were highly correlated with southerly winds from the heavily infested Laguna district of Mexico, 192 miles (320 kilometers) away.

Using an airplane equipped with sampling nets, a number of studies of pink boll-

worm moth dispersal were made in Mexico in 1928. Pink bollworm moths were collected at altitudes of up to 984 yards (900 meters) (Glick, 1939). Similar flights over the Rio Grande Valley resulted in the collection of pink bollworm moths at altitudes ranging from 32 to 328 yards (30 to 300 meters) (Glick, 1957). Glick (1967) concluded that pink bollworm infestations in the United States were spread by moth migrations from Texas and Mexico.

Establishment of the pink bollworm in central Arizona after 1958, and the detection of infestations in southern California in 1965, increased concern about further spread into the San Joaquin Valley of California. Sharma *et al.* (1971) demonstrated pink bollworm moth catches in hexalure-baited traps placed in fallow and sorghum fields in the Imperial Valley at distances ranging from 10 to 164 yards (10 m to 150 meters) from cotton fields. The dispersal potential of pink bollworm under arid desert conditions was demonstrated by Bariola *et al.* (1973) who captured moths in four acres (1.6 hectares) of isolated cotton in the Mojave Desert 33 miles (55 kilometers) from the nearest infested cotton. Male moths were caught in hexalure-baited traps the last of May, and 6 days before first cotton flowers opened. The first larva was found in a flower on June 2, indicating the infestation resulted from oviposition by moths (immigrating at least 33 miles [55 kilometers]) which had overwintered as larvae. Kaae *et al.* (1977) also reported early season movement of pink bollworm in southern California. Manley (1986) identified both early- and late-season dispersal of pink bollworm males in Arizona using gossyplure-baited traps placed in desert habitats from 0.96 to 7.2 miles (1.6 to 12 kilometers) from cotton. The author suggested that crop phenology resulted in the observed dispersal patterns.

Stern (1979), reported pink bollworm male moth catches in gossyplure-baited traps in the desert between the Imperial, Coachella and Palo Verde Valleys of California from late-June through mid-November. These valleys are approximately 48 to 72 miles (80 to 120 kilometers) apart. One area with a large number of captured moths was approximately 19.2 miles (32 kilometers) from the nearest cotton. Graham (1978) reported that pink bollworm moths migrated approximately 24 miles (40 kilometers) from infested cotton in the same area. Stern (1979) also collected a high number of pink bollworm moths during mid-september in the Riverside-Mojave Desert area over 96 miles (160 kilometers) north of Palo Verde, Coachella and Imperial Valleys. The largest number of moths were caught following southwesterly wind and rain storms. Beasley *et al.* (1985) placed gossyplure-baited traps about every 3.6 miles (6 kilometers) between the Palo Verde and Imperial Valleys. Traps on each end of the trapline were about three miles (five kilometers) from cotton. Pink bollworm moth catches showed a small peak in late April and early May, declined after a small peak in June through July, and increased dramatically in late August. Moth trap catches in the desert corresponded to fluctuating population trends in commercial cotton fields. High moth catches in the desert early and late in the season suggested migrating individuals from the emerging overwintering population and a dispersal late in the season. Pink bollworm moth emergence in cages and male moth catches in gossyplure-baited traps have been shown positively related to

temperature and variability of wind direction and negatively related to wind speed (Beasley *et al.*, 1985; Adams *et al.*, 1987).

Native pink bollworm moths have been caught in pheromone-baited traps in the uninfested San Joaquin Valley of California each year since 1968 (USDA, Animal and Plant Health Inspection Service, unpublished reports). Moths that were caught in these traps were strongly suspected to be migrants from southern desert valley cotton growing areas, as much as 384 miles (640 kilometers) away. Wolf and Kauper (Unpublished data, Wayne W. Wolf, United States Department of Agriculture, Agricultural Research Service, Georgia Coastal Plains Experiment Station, Tifton, Georgia; Erwin K. Kauper, Metro Monitoring Service, Covina, California) conducted trajectory analysis from southern California from wind data to determine the occurrence of weather systems that could transport pink bollworm moths from the southern Coachella and Imperial valleys to the central California San Joaquin Valley. Their data show that favorable windflows were present when low pressure areas occurred off the southern California coast for approximately two days. Weather systems favorable for moth dispersal occurred ten times during a selected 13-month sampling period. This provided 25 days for potential migration.

An aggressive program involving cultural control and sterile moth releases appears to have been successful in preventing the establishment of the pink bollworm in the San Joaquin Valley. Noble (1936) showed that, after exposure for one to seven days to simulated conditions for El Paso, (altitude of 2952 feet [900 meters] and average temperature of 60F [15.5C]), pink bollworm moths resumed oviposition of fertile eggs. Also, studies have shown that the pink bollworm can overwinter in California's San Joaquin Valley (Personal Communication, A. C. Bartlett, Western Cotton Research Laboratory, USDA, ARS, Phoenix, Arizona; R. T. Staten, Methods Development Laboratory, USDA, APHIS, Phoenix, Arizona) and the Antelope Valley of California, where an average air temperature of 20F (-7.2C) occurred, and the ground was frequently frozen during December and January to a depth of three to four inches (7 to 10 centimters) (Stern 1979).

Although much of the evidence for migrating pink bollworm moths is indirect, and based on infestations or trap catches at distances from known sources of infestations, more definitive information to support moth dispersal as a source of spread and establishment of the insect has been documented. Flint *et al.* (1975b) released P^{32} radiolabeled pink bollworm moths in a cotton field and determined that they dispersed an average of about 65 yards (60 meters) from the release point within 11 to 12 hours. Under tethered, flightmill conditions, pink bollworm moths flew the equivalent of 13.2 miles (22 kilometers) during a 24-hour period at an average speed of about 0.36 miles per hour (0.6 kilometers per hour) (Flint *et al.*, 1975a). The majority of the live male moths that were captured in cotton, alfalfa, sugarbeet and desert habitats, and marked with fluorescent dyes, were recaptured within the habitat in which they were released (Flint and Merkle, 1981). These authors also reported that from 18 to 21 percent of the moths that were originally captured in desert, alfalfa and sugarbeet habitats were recaptured in cotton after they were marked and released; only 4.7 percent of the moths

that were released in cotton were recaptured in other habitats. These data suggest greater movement to cotton than from cotton during April and May.

The attractiveness of cotton over non-host habitats was further substantiated by Flint *et al.* (1987). They found that pink bollworm moth catches in gossyplure-baited traps were equally distributed in cotton, corn, alfalfa, wheat, pea and grape habitats until approximately one week prior to cotton flower bud formation. Following flower bud formation the number of moths caught in cotton fields increased dramatically, but not in non-host crop fields. Butler *et al.* (1983), found that both male and female pink bollworm moths moved into and out of cotton fields throughout the season. Catches of virgin and mated females suggest that both young as well as older females were dispersing. The mating status of dispersing pink bollworm populations is of critical importance in population dynamics of the species. Although Kaae and Shorey (1973) found male pink bollworm moths in field crops adjacent to cotton, no mating pairs were observed. However, indirect evidence obtained by placing mating stations in desert habitats indicate that pink bollworm moths mate as well under those conditions as in cotton habitats (Flint and Merkle, 1981).

Van Steenwyk *et al.* (1978), showed that pink bollworm moths marked with rubidium were highly mobile within a 10-acre cotton field from July to October. Rubidium-marked moths left the fields primarily in September and October and were captured as far as one mile from the field. Rubidium-marked moths from overwintering larvae departed from the cotton field from May through June. This corroborates the indirect evidence that pink bollworm migrate following emergence from the overwintering population (Bariola *et al.*, 1973; Beasley *et al.*, 1985), as well as late in the season (Ohlendorf, 1926; McDonald and Loftin, 1935; Beasley *et al.*, 1985).

Bartlett (1985) released laboratory-reared, dominant, dark body color pink bollworm moths (sooty strain) in cotton. Released male moths were recaptured within 24 hours in gossyplure-baited traps placed one mile from the release point. A small number of the moths were recovered up to 23 days after their release. In other studies (Bartlett and Lingren, 1984), most recoveries of released, sooty male moths occurred in gossyplure-baited traps placed downwind from the release point, suggesting the influence of wind on moth dispersal.

Short-range movement of pink bollworm moths within a cotton crop that is associated with mating and reproduction has not been studied extensively in spite of its importance in pink bollworm population dynamics. Lingren *et al.* (1978), using night vision goggles, observed pink bollworm males moving crosswind from 30 minutes to one hour before mating was observed. When males intercepted pheromone plumes from lures, they oriented upwind toward the source. In most cases, the pheromone plume did not extend over 16 yards (15 meters) from a lure, indicating that the crosswind flight is a searching mechanism to increase a male's probability of intercepting a pheromone emitting female moth. The authors also observed females moving from plant to plant while touching extended phermone glands to leaf surfaces. Presumably this "pheromone marking" aids the male in locating the receptive female. Lingren (1983) observed newly eclosed (emerged) pink bollworm moths taking short flights of

about one yard (one meter). During a second period of flight activity from three to six hours after eclosion (emergence), moths flew from one to two yards (one to two meters) with about 10 percent flying beyond viewing range. About 11 hours after eclosion most moths flew out of viewing range.

Short-and long-range flight activities played a major role in the spread and establishment of pink bollworm infestations in the United States and Mexico, and probably in other areas of the world as well. Short-range and interfield movements appear to occur at random except for directed orientation toward sex pheromone sources. Long-range movement appears to be primarily influenced by wind speed and direction. Most of the evidence for pink bollworm dispersal has been obtained indirectly. Some factors, such as cotton crop phenology, temperature, wind speed and direction and short-range attraction to the sex pheromone, gossyplure, appear to influence pink bollworm moth movement. However, the effect of these factors on dispersal have not been quantified. Also, estimates have not been made on what percentage of the population disperses during periods of flight activity. The importance of documenting the role of dispersal in the population dynamics of the species, and its implications for the development of new control technology justify extensive, in-depth research.

BOLL WEEVIL

ORIGIN AND DISTRIBUTION

The boll weevil, *Anthonomus grandis grandis* (Boheman), originated in Meso-America (southern Mexico and Central America) on plants of the malvaceous genus *Hampea* (Burke *et al*., 1986). The boll weevil had probably achieved its present distribution in western Mexico and southern Arizona, as well as in northeastern Mexico, before the beginning of primitive cotton cultivation. Circumstantial evidence for migration of the boll weevil in the United States was obtained by documenting the extension of its range each year after the initial infestation in Texas in 1892. From 1894 to 1922, the boll weevil extended its range from 39 to 154 miles (65 to 258 kilometers) annually, (Hunter and Hinds, 1905; Hunter and Coad, 1923), and crossed non-cotton habitat extending for more than 39 miles (65 kilometers) to infest cotton.

FLIGHT ALTITUDE AND DISTANCE

Several techniques, including aerial netting, flight screens, pheromone traps and isolated cotton plots, have been employed to document the altitude at which and distance the boll weevil may move. An airplane equipped with an insect collection device was used by Glick (1939), Glick (1957) and Glick and Noble (1961) to collect the boll weevil at various altitudes over Texas and Louisiana. Boll weevils were collected during the day flying at altitudes from 6 to 667 yards (5.5 to 610 meters) from August to November. Only one weevil was collected flying at night.

Gaines (1959) captured boll weevils on 0.98 X 1.6 yards (0.9 X 1.5 meters) sticky coated flight screens from 0.98 to 18 yards (0.9 to 17 meters) above the ground with about one-fourth of the specimens collected from the lowest screens. There was a significant correlation between the number of weevils collected and the altitude of the

screens. Over 50 percent of weevils that were captured on flight screens while flying from hibernation sites in South Carolina during April to July were captured at altitudes of less than three yards (2.8 meters); only nine percent were caught above 13 yards (12.4 meters) (Taft and Jernigan, 1964). Weevils flying from a cotton field from August through December were caught at a greater height, with about 39 percent being caught above 13 yards (12.4 meters).

Rummel *et al.* (1977) used pheromone traps placed at heights of 0 to 9 yards (0 to 8.3 meters) and captured over 90 percent of the overwintered weevils flying below five yards (4.6 meters). However, during the late-summer and fall dispersal period, the number of boll weevils captured at the nine yards (8.3 meters) level increased from eight- to ten-fold. Rummel *et al.* (1977) also captured weevils at an altitude up to 133 yards (122 meters) with aircraft-towed nets during the fall of 1973.

The distance that the boll weevil may fly has been empirically determined by: (a) its flight to isolated plots or pheromone traps, (b) its movement from overwintering habitat to cotton, and (c) the capture of marked adults. Beckman and Morgan (1960) reported weevils moved into a cotton plot on St. Simon Island, South Carolina, that was about 24 miles (41 kilometers) from the closest cotton. Rummel and Adkisson (1970) found that most cotton fields infested by the boll weevil were adjacent to favorable overwintering habitat. This indicated that they were not moving great distances from overwintering habitats to the fields. Fye and Parencia (1972) found that infested cotton fields located more than about four miles (8 kilometers) from infested *Thurberia* plants in Arizona usually did not become reinfested in successive years. Fields adjacent to infested *Thurberia* plants were infested every year. In Mexico during October of 1968, Davich *et al.* (1970), using sticky-coated wing traps baited with males, captured weevils up to 43 miles (73 kilometers) from the nearest cotton. There was no indication that prevailing winds, topographical features or storms influenced movement and subsequent capture of boll weevils. Roach and Ray (1972) found in South Carolina that boll weevils from the F_1 and succeeding generations move more than 19 miles (32 kilometers) in numbers large enough to damage cotton. Pieteri and Urban (1977) captured numerous boll weevils in traps within 3.3 miles (5.6 kilometers) of cultivated cotton on the mainland; relatively few weevils were caught on Padre Island (Texas), about 2.88 miles (4.8 kilometers) from cultivated cotton; and no weevils were trapped on oil platforms in the Gulf of Mexico, more than seven miles (12 kilometers) from cultivated cotton. The lack of favorable transport systems toward the ocean probably limited flight in that direction.

Although Johnson *et al.* (1976) captured two marked boll weevils 43 miles (72 kilometers) from the point of release in Mississippi, 88 percent of the marked boll weevils were captured within 14 miles (24 kilometers) of the release point. The direction of dispersal was evenly distributed from the release point. Dickerson and Leggett (Unpublished data, W. A. Dickerson, North Carolina Department of Agriculture, Raleigh, North Carolina) captured a marked boll weevil in a cotton field D-vac sample in North Carolina that was 63 miles (105 kilometers) from its South Carolina release point.

SEASONAL MOVEMENT

A knowledge of the seasonal pattern of movement of boll weevils is important for timing cultural and chemical control strategies. Variability in the seasonal pattern of weevil movement in the cotton growing areas could be due to genetic differences in populations, climatic variations, cultivars of cotton, plant phenology, or cultural practices.

Early-season and Within Field — Many studies have documented the temporal pattern of boll weevil emergence from overwintering habitats (Fenton and Dunnam, 1929; Gaines, 1935; Davis *et al*., 1967; Davis *et al*., 1976; Ridgeway *et al*., 1971; Roach *et al*., 1971). Generally, overwintering emergence occurs between April and June. Boll weevil movement, as well as the stimuli which induce movement, varies with seasonal changes in the cotton plant, with the age structure of the population of boll weevils and with the populations physiological condition.

White and Rummel (1978) found that very few overwintered weevils entered presquaring cotton in Texas but immigration increased with maturity and number of squares. Pheromone traps consistently indicated peak flight activity of overwintered boll weevils occurring during May or early June. Ridgeway *et al*. (1971), using male-baited sticky wing traps, observed a cessation of movement in mid-June that is accompanied by the accumulation of boll weevils in cotton fields. They speculated that the presence of cotton or the age of cotton may not be the principal factor governing its seasonal movement. Further, Rummel and Bottrell (1976) found a similarity in weevil response to isolated plots of cotton and pheromone-baited traps away from cotton. They concluded that the presence of pheromone-producing male weevils in cotton was not a major causal factor in the decline of weevil response to traps. However, McKibben *et al*. (1977) determined that volatile compounds from the cotton plant attracted both overwintered and late-season migrating boll weevils in Mississippi. They concluded that plant attractants are not as important as the male pheromone in inducing the boll weevil to fly.

Within Field — Following their entry into attractive cotton fields, much of the movement by boll weevils is associated with mating, and finding suitable feeding and oviposition sites. Cross and Mitchell (1966) observed in the field that male boll weevils did not respond to females over a distance of greater than 1 to 2 inches (2.5 to 5 centimeters). However, females often sought males at a distance of more than 9.8 yards (9 meters) especially when the males were upwind. Hardee *et al*. (1969) found that females responded to males from a distance of 90 yards (82 meters) in a cotton field. Boll weevil oviposition occurs primarily during the day from 0900 to 1500 hours (Howe, 1916). McGovern *et al*. (1987) found that females moved more when searching for pristine squares in heavily infested fields. Females normally reject squares with an egg puncture and continue searching for uninfested ones. Other behaviors associated with in-field movement of boll weevils as effected by abiotic factors, such as temperature, rain and wind and biotic factors such as cotton cultivars were reported by Gilliland and McCoy (1969), Jones and Sterling (1978), Mitchell and Mistric (1965) and Mitchell *et al*. (1972).

Mid-to Late-Season Dispersal — Fenton and Dunnam (1928), Taft and Jernigan (1964) and Hopkins *et al.* (1971) observed a general mid-season dispersal of boll weevils, even in slightly infested fields from mid-June through August. Several factors appeared to have influenced their dispersal behavior. Fye and Bonham (1970) observed that a lack of oviposition sites triggered dispersal when populations increased to a level where there was less than one unpunctured square per pair of weevils. Guerra (1986) released marked boll weevils in Texas that had been reared from squares or bolls. He indicated that square-reared weevils were physiologically oriented toward feeding and oviposition rather than flight from cotton. In contrast, boll-reared weevils exhibited a tendency to disperse when they were released either in or out of cotton fields. Mitchell and Mistric (1965) observed that squares and bolls in newly infested fields receive an unusually large number of egg punctures, indicating an immigration of reproductive females. Cross (1976) found that the capture of dispersing weevils in traps outside of cotton began the first week of August in south Mississippi.

ENTRY INTO OVERWINTERING HABITAT

Wade and Rummel (1978) examined leaf litter in the rolling plains of Texas from August 1975 to March 1977 and found that most overwintering weevils move into hibernation sites in October and November. Apparently, only a small percentage of a diapausing population enters an overwintering habitat during late August and early September. However, Gaines (1935) found weevils in Spanish moss as early as September 1 in Mississippi. Most studies have indicated that weevils fly a relatively short distance to enter a hibernation habitat. Up to 90 percent of the hibernating weevils are located within 55 yards (50 meters) of cotton field edges (Bondy and Rainwater, 1942; Beckham, 1957; Fye *et al.*, 1959).

Diapausing boll weevils that enter leaf litter may not remain in one spot throughout the winter. Some move in response to changing stimuli such as temperature and moisture. Hopkins *et al.* (1972) observed that boll weevil movement in overwintering habitat increases as litter moisture rises. Mitchell (1971) found that diapausing boll weevils marked with P^{32} and placed in leaf litter in Mississippi did not move more than 24 inches (61 centimeters) from their original release point during January and February. In March and April, nine weevils moved more than 5.6 yards (5.2 meters) and one male moved 15 yards (14 meters). Some weevils moved quite extensively without moving very far from their release point.

WHITEFLY

Species of whiteflies infesting cotton in the United States include the iris whitefly, *Aleyrodes spiraeoides* (Quaintance); bandedwinged whitefly, *Trialeurodes abutilonea* (Halderman); greenhouse whitefly, *T. vaporariorum* (Westwood) (Byrne and von Bretzel, 1987; T. F. Leigh and J. B. Graves, Personal communication, Department of Entomology, Louisiana State University, Baton Rouge, Louisiana); and the sweetpotato whitefly, *Bemisia tabaci* (Gennadius). Whiteflies are generally characterized as

occasional or sporadic pests of cotton in the United States, but the sweetpotato whitefly has become a pest of increasing importance since 1981 (Duffus and Flock, 1982; Johnson *et al*., 1982). Because sweetpotato whitefly damages cotton both directly and indirectly, steps now are commonly taken to reduce its populations. When dense populations occur sweetpotato whitefly may extract enough plant material to reduce yields. Also, the honeydew from large populations of this pest may interfere with photosynthesis and serve as a medium for a lint-staining sooty fungi. Finally, sweetpotato whitefly serves as a vector for cotton leaf crumple virus (Brown and Nelson, 1984).

The sweetpotato whitefly was first described in 1889 on tobacco in Greece. Outbreaks were reported on cotton in India in the 1920s (Husain and Trehan, 1933). The sweetpotato whitefly subsequently spread throughout the Near and Far East and Central and South America (Horowitz, 1986). In each country where this whitefly has appeared, its presence initially is of little consequence but, after one or two years, populations become epidemic. Although reasons for sudden outbreaks remain unclear, they probably are related to a rapid increase in pesticide resistance, the impact of pesticides on natural enemies and changes in agronomomic practices, such as the extension of cropping seasons (Gameel, 1969; Dittrich *et al*., 1986; Von Arx *et al*., 1983; Meyerdirk *et al*., 1986).

Whiteflies have a unique life cycle. Despite the fact that they experience incomplete metamorphosis, the immatures are called larvae because they develop an apparant "pupal" case. Eggs, commonly laid on the underside of leaves, hatch into first instar larvae which are mobile. These "crawlers" seldom move more than a few inches and soon settle to feed, almost always on the leaf where the egg was laid. The subsequent second, third and fourth instars are sessile (immobile). Adults emerge from "pupal" cases and, after a brief teneral period (time of hardening of the exoskeleton), are capable of flight. Movement of any spatial consequence is limited to the adult stage.

Because whiteflies are tropical insects (Mound and Halsey, 1978), they obviously moved by some means to the temperate areas which they now inhabit. We have no evidence, however, that whiteflies routinely engage in the long- range migration common to other homopterous insects (Taylor, 1985).

Whiteflies may migrate shorter distances of up to 3 miles (5 kilometers) (Coudriet *et al*., 1986; Cohen *et al*.,1986) and dense populations are routinely seen over fallow ground (Gerling and Horowitz, 1984; Byrne *et al*., 1986). If the Southwest cotton production system serves as an example, short-range movement is apparently all that whiteflies require for survival and reproduction once they become established in an area.

In the Southwest, whiteflies overwinter in populations as actively developing individuals rather than as populations of individuals in reproductive diapause. Coudriet *et al*. (1985) found active individuals throughout the winter months in the Imperial Valley of California, and D. N. Byrne (unpublished data) made similar observations in Arizona. These insects are commonly found on *Malva parviflora* L. and annual sowthistle, *Sonchus oleraceus* L. from October until March, and on common sunflower, *Helianthus annuus* L. and field bindweed, *Convolvulus arvensis* L., in the spring. Similarly, Gameel (1969) reported that large populations of whiteflies over-

winter on weeds along river banks in Sudan. In Isreal, Gerling (1984) found sweetpotato whiteflies, using 19 plant species as winter hosts, as follows: *Abutilon grandifolium*; *Lantana camara*; *Chrysanthemum indicum*; little mallow, *Malva parviflora* L., *Gebera* spp.; *Solanum vilosum*; *Withania somnifera*; *Celtus australis*; *Loniora etrusca*; *Verbena* spp.; *Circis siliquestram*; field bindweeds; *Plumbago europaea*; *Alcea setosa*; *Tropaeolum majus*; *Calendula* spp.; and annual sowthistle. Just as in the United States, plants of some species (for example, *Lantanta camara*, *Abutilon grandifolium* and *Chrysantemum indicum*) have abundant foliage and harbor sweetpotato whitefly throughout the year; others (like annual sowthistle, *Tropaeolum majus* and *Celtus australis*) serve only as seasonal hosts.

In the Southwest, whiteflies infest a number of both crop and weedy plant species. Coudriet (1985) believes lettuce is one of the more favorable hosts since it is planted as early as August and harvested through March. Moreover, the development time for the sweetpotato whitefly on lettuce was the second shortest (19.4 days) of the 17 crop species tested. He stated that in the field, the sweetpotato whitefly completes one generation and starts another between late October and early January. Spring crops such as watermelon and cantaloupe are planted for June harvesting while alfalfa is grown year round. Cotton, the principal host for whiteflies, is planted in late March and picked at year's end. Bionomics of the sweetpotato whitefly, are similar in the Near East (Gerling, 1984) and India (Husain *et al.*, 1936), where populations overwinter on a variety of cultivated and wild plant species before moving to spring hosts such as potato and cultivated sunflower. In every situation where whiteflies are a serious problem, wild and cultivated hosts grow in close proximity and whiteflies have little difficulty finding new habitats when existing habitats become less preferred.

The sequence of events in the Southwest, which mirrors that in other parts of the world, follows a routine pattern: existence at a low level on wild or cultivated host from January through May (Coudriet, 1985); migration to early spring vegetables, such as cantaloupe, where they remain through mid-summer (Byrne, unpublished data); and movement to cotton in July and August where populations begin to build exponentially. Cotton, by far, produces the greatest number of whiteflies, considering the acres grown and the large amount of biomass it provides for oviposition and feeding sites. Furthermore, cotton is present at a time of year when environmental conditions favor population increase. In the fall, whiteflies move to newly emerged vegetables, such as lettuce where they remain until populations decline in November. Abundant suitable hosts are never lacking, but cotton contributes so prominently to the proliferation of whiteflies in the Southwest that this insect is now identified by many as a principal cotton pest.

Observations show that whiteflies accomplish their short-range aerial movements similar to aphids and other small insects (Haine, 1955). In examining the relationships among body mass, wingbeat frequency and wing loading in insects, Byrne *et al.* (1988) showed that larger, strong-flying insects seemingly use strategies, such as compensating for high wing loading with higher wingbeat frequencies similar to other flying animals. Accordingly, wingbeat frequencies and wing loading correlation

coefficients are highly significant for all groups of insects weighing more than 0.03 grams. In small insects (mass < 0.03 grams) no such relationship was found between wing loading and beating frequency. This suggests that these species are inherently weaker fliers. Several whitefly species examined had mass ranging from 3.3 to 8.0 X 10^{-5} grams, a wingbeat frequency ranging from 165.6 to 224.2 hertz (Hz) (cycles per second) and a wing load from 2.12 to 5.23 X 10^{-3} grams per square centimeter. These data indicate whiteflies are poor fliers and that flight is accomplished through mechanisms such as clap-and-fling wing movement which produce a high drag coefficient.

Weak-flying whiteflies are adrift in abundance during certain periods of the day. Sixty percent of adult whiteflies captured in Isreal was over fallow ground (Gerling, 1984), indicating that flying whiteflies are widespread when populations are high. Byrne *et al*. (1986) recorded similar results in Arizona. Daytime movement is periodic, resembling aphid activity (Johnson *et al*., 1957). When Byrne and von Bretzel (1987) examined the flight activity of sweetpotato and bandedwinged whiteflies in a cotton-growing region of Arizona, they found a definite rhythmicity. Aerial populations consistently exhibited peaks, with the majority (> 60 percent) of flight activity taking place within approximately the same four-hour period each day. The distinct periodicity of flight might be explained by the fact that adult emergence (> 90 percent) occurs within the first hour after photophase with a teneral period (time of exoskeleton hardening) of slightly more than four hours at 80F (27C).

Whiteflies appear to have evolved behavioral and physiological processes, such as time of emergence and first flight, to minimize mortality during migration. An optimal time of emergence exposes the insects to temperatures which speed certain physiological processes and minimizes the teneral period, when whiteflies are particularly vulnerable because they are unable to fly. In southwestern United States, an optimal eclosion allows the adults to avoid being airborne during the hours of the greatest heat. Dawn emergence appears to afford whiteflies some of the best aspects of both strategies.

A great deal of movement, termed trivial flight by Southwood (1962), takes place within the crop boundary layer. Presumably, insects in trivial flight primarily are searching for feeding and oviposition sites. However, whiteflies are inclined not to leave the plants on which they originate, especially if conditions are favorable for their survival. The extent to which whiteflies fly within a cotton field was examined by Gerling and Horowitz (1984) using flat white sticky traps. They found that traps placed at canopy height caught 17 times more whiteflies on the upper trap surface than on the lower surface. Further, by comparing whitefly capture on traps placed on the ground and at canopy height and by isolating plants near traps using cardboard partitions, they found that all captured whiteflies did not originate upon the plants immediately above the traps.

Gerling and Horowitz (1984) surmised that whiteflies leave cotton foliage due to age-correlated dispersive behavior or in search of better feeding or oviposition (egg laying) sites. Apparently, dispersing whiteflies are attracted to colors of short wavelength (Mound, 1962; Combe, 1982) which results in ascending flight behavior. However, whiteflies in search of better feeding and oviposition sites apparently fly beneath the cotton canopy, as shown in the partition experiment of Gerling and

Horowitz (1984). Whiteflies flying above two yards (two meters) apparently do not recognize host plants before beginning their descent; hence, airborne individuals may land on bare soil. If they happen to reach a plant canopy, they disperse among the plants and search for suitable feeding and oviposition sites (Prokopy and Owen, 1982). If the whiteflies descend to bare ground, they may fly about looking for a proper substrate upon which to land. Apparently, they recognize suitable hosts by color because they tend to accumulate on yellow traps.

Most whitefly movement studies have been conducted within areas where populations inhabited agricultural communities, within which the insects moved freely from plant to plant, crop to crop or weed to crop. Whiteflies also are capable of long-range movement under favorable conditions, but reports of such movement are rare. Once established in an area, whitefly movement appears to be primarily associated with feeding, reproduction and the search for attractive host plants.

SPIDER MITE

Spider mites disperse aerially and by crawling on the plant (Kennedy and Smitley, 1985). Intra-plant movement occurs as pre-reproductive females move to uninfested areas of the plant (Hussey and Parr, 1963; Mitchell, 1973). Inter-plant dispersion occurs in response to environmental and biological cues, such as desiccation of, or damage to, host plants (McEnroe and Dronka, 1971), overcrowding (Boyle, 1957; Hussey and Parr, 1963; Smitley and Kennedy, 1985), increasing predatory activity (Bernstein, 1984), and repellent effects of pesticides (Gerson and Aronowitz, 1981; Iftner and Hall, 1983; Penman and Chapman, 1983; Franklin and Knowles, 1984; McKee *et al.*, 1987). Dispersal behavior of the twospotted spider mite, *Tetranychus urticae* Koch, involves movement up the plant and, if wind is present, orientation away from light and raising of the forelegs (Suski and Naegele, 1966; McEnroe and Dronka, 1971; Boykin and Campbell, 1984; Smitley and Kennedy, 1985). Because of their buoyancy, spider mites can be carried to great heights (Coad, 1931) and for long distances (Johnson, 1969). Thus, there is great potential for spider mite movement from rapidly increasing populations in one crop to another. Such movement has a strong impact on spider mite management (Brandenburg and Kennedy, 1982; Kennedy and Margolies, 1985; Margolies and Kennedy, 1985; Miller *et al.*, 1985).

In the San Joaquin Valley of California, three species of spider mites are key pests of cotton: strawberry spider mite, *Tetranychus turkestani* Ugarov and Nikolski; twospotted spider mite; and the Pacific spider mite, *Tetranychus pacificus* McGregor (Leigh, 1963; Leigh and Burton, 1976; Leigh, 1985). Cotton is plowed under each fall in California and few, if any, weeds remain on which the spider mites can overwinter. Yet, spider mites frequently appear on cotton within one week of its emergence (April-May) and in a relatively random distribution. Colonizing spider mites during the early part of the growing season may be emerging from the soil or moving from nearby weeds. However, it is more likely they are arriving aerially from neighboring crops.

All three spider mite species may be found in an individual cotton field. Surveys of the San Joaquin Valley indicated strawberry spider mite is the dominant species in the early season, with the twospotted spider mite dominant in the mid-season, while the Pacific spider mite is present in 42 to 50 percent of the fields sampled (Grafton-Cardwell *et al.*, 1987). However, when the cotton field is located next to almond orchards, the Pacific spider mite is present in 85 percent of the fields (E. E. Grafton-Cardwell., unpublished data). Thus, perennial plants such as almond act as significant overwintering hosts for spider mites in the San Joaquin Valley. Where cotton is located downwind (or south) of almond, significantly more Pacific spider mites are found in the north half than in the south half of the field throughout the season (E. E. Grafton-Cardwell, unpublished data). Almond appears to serve both as an early season and a continuous host for supplying Pacific spider mites for infesting cotton. Whatever the source, the earliest spider mite colonizers rapidly distribute themselves within and between cotton plants (Carey, 1982; Carey, 1983; Wilson *et al.*, 1983).

During most of the growing season, cotton acts as a recipient of, and not a source for spider mite dispersion. This is because the biological and environmental cues which stimulate large-scale dispersion are not present until the end of the cotton growing season. Since cotton continuously produces new foliage and is usually well irrigated, the problems of desiccation and crowding of the spider mites, characteristics that stimulate dispersal from other crops, do not occur as frequently in cotton. Further, the use of a non-repellent such as the acaracide dicofol (Kelthane®) in cotton does not stimulate the mites to move. The spider mite populations that develop on cotton also tend to inhabit the middle region of the plant through most of the season and the mites are not exposed to wind velocities that would aid in their dispersal (Carey, 1982).

In contrast to cotton, almond trees frequently experience water stress and only produce one set of foliage per season. Since the food source is limited and the almond trees desiccate as a result of water stress, high density spider mite populations shift into a dispersal mode. The occasional occurrence of dense populations of predatory mites may also cause spider mite dispersal from almond. In addition, the acaricides used to control spider mites in almond—propargite (Comite®, Omite®), cyhexatin and hexakis (Vendex®, Torque®) as well as several pesticides used for insects (some pyrethroids and carbamates) are highly repellent to spider mites and stimulate aerial dispersal (Iftner and Hall, 1983; Fisher and Wrensch, 1986; Penman *et al.*, 1986). Thus, almond can be a significant source of sudden, large-scale, aerially dispersing Pacific spider mites and predatory mites throughout the cotton growing season (E. E. Grafton-Cardwell, unpublished data; Hoy, 1982; Hoy *et al.*, 1985). These peaks of dispersion may negatively affect chemical control of spider mites in cotton by increasing the spider mite density above the economic injury level of about seven mites per leaf. However acaricides are usually sufficiently efficacious to reduce spider mites in cotton below the economic threshold.

Many horticultural and field crops, such as melons, beans and corn support high densities of spider mites as they are dried out for harvest (July and August). Although chemical control of spider mites frequently is not required in these crops, drying stim-

ulates spider mite dispersion into neighboring cotton (E. E. Grafton-Cardwell, unpublished data) and causes a second cycle of mite problems in the cotton that may need additional chemical treatments. Spider mites have their greatest impact on cotton in early- to mid- season (Furr and Pfrimmer, 1968), and the late-season dispersion is considered less important. Season influx also is less important.

Defoliation of the cotton at the end of the growing season, and hence the loss of the spider mite food, probably stimulates the mites to disperse and crawl under cover vegetation and the bark of perennials such as almond to overwinter. This may explain why almond may occasionally host an early-season population of dicofol (Kelthane®) resistant spider mites even though dicofol is not used in almond.

PLANT BUG

Several species of plant bugs in the family Miridae that attack cotton appear to be highly mobile with infestations appearing and disappearing within two or three days. Plant bugs usually are seen in the terminals of plants as well as actively flying near sunrise and sunset suggesting a crepuscular (faint light, i.e. daybreak and twilight) flight activity. With the aid of a black light, western lygus bug, *Lygus hesperus* (Knight), can be observed resting and feeding in the terminals of plants at night. When disturbed in the day, adults readily fly but usually to a near plant.

Infestations of cotton by plant bugs are commonly associated with nearby native weed and crop hosts (Smith, 1942). Among the crop hosts of the western lygus bug are alfalfa (Stern *et al*., 1964) (whether grown for hay or for seed), safflower, (Mueller and Stern, 1974) and beet grown for seed. Weed species in crops, and many native plants such as annual fleabane, *Erigeron annuus* (Pers.), (Fleischer *et al*., 1987) also serve as hosts for western lygus bug. In arid areas western lygus bug may be a more consistent pest near riparian outflows from mountains. Severity of infestation, often expressed as crop damage, is reported to be greatest in parts of a field that lie adjacent to an alternate host. Schowalter & Stein (1987), Stern *et al*. (1964, 1967) and Sevacherian and Stern (1975) reported that local movement of western lygus bug involves field-to-field movement. Stride (1968) reported a similar relationship between *Lygus vosseleri* Poppham and its native and crop hosts in Uganda. Fleischer *et al*. (1987) stated that movement of the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) from its weed hosts to cotton is largely a diffusion process similar to the flight behavior recorded for the cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter) by W. L. Sterling (Personal communication, W. L. Sterling, Department of Entomology, Texas A&M University, College Station, Texas). We are not aware of any long-range movement studies with plant bugs. However, infestations of the western lygus bug commonly develop in fields in desert areas isolated by several miles from known sources of infestation (T. F. Leigh, personal observation).

Principal natural enemies of mirid plant bugs are several generalist predators including several spiders (Araneida) (Whitcomb *et al*., 1963; Dean *et al*., 1987), *Geocoris* spp., *Nabis* spp. and *Orius* spp., bugs and mymarid and euphorid parasites (Clancey,

1968). Species of these natural enemies are found in native vegetation, weed and crop plants used as hosts by lygus bugs (Fleischer and Gaylor, 1987). Movement of plant bug predators and parasites such as *Anaphes ovijentatus* (Crosby & Leonard) and *Leiophron uniformis* (Gahan) (Graham *et al.*, 1986) appear not to be highly migratory since they are localized in the areas with high densities of plant bug host plants.

SUMMARY

A review of the literature pertaining to the short- and long-range movement of insects and mites attacking cotton is presented. The impact of local dispersion between fields, crops and native vegetation is discussed relative to the development of insect suppression techniques. The impact of long range migration by insects between regions acting as source areas and recipient areas is also presented. The discussions point out the need for a thorough understanding of the movement capabilities of cotton pests for developing technologies that require the use of less pesticides and that may be applied on an areawide basis.

Chapter 5

BIOLOGY, ECOLOGY AND EPIDEMIOLOGY OF MICROBIAL ORGANISMS INFECTING ARTHROPOD PESTS

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INTRODUCTION

Cotton is host to a multitude of insect and mite pests, most of which are known to be infected by one or more entomopathogens. These include viruses, bacteria, fungi, protozoa and entomophagous nematodes. Knowledge of pathogens on these pests is considerable but is far from complete. New host-pathogen relationships, even new groups of pathogens, are still being discovered. The purpose of this chapter is to summarize knowledge of the entomopathogens encountered in pest populations in the cotton field. Their biology, symptomatology, pathology and epidemiology will be discussed as appropriate for each pathogen and host species relationship. This chapter is organized according to pathogen groups rather than pest species in order to prevent redundancy. Each pathogen group shares certain features which do not differ greatly from host to host. Therefore, the general biology of each group will be presented and followed, where appropriate, by special considerations related to specific hosts.

In reviewing the literature on pathogens of cotton pests, it is immediately apparent that, while most cotton pest species have been identified as hosts for various pathogens, relatively little of the research effort on these host- pathogen relationships has been conducted in the cotton system. A great deal of present knowledge of these pathogen-host relationships comes from research efforts on crops such as corn, soybeans, sorghum, vegetables and others. The demand for high levels of control of key cotton pests such as the boll weevil and the bollworm/tobacco budworm have resulted in heavy reliance on chemical insecticides in the past. Because of this dependency there has been relatively little effort made to survey for the pathogens of arthropod pests of cotton or to learn of their actual or potential roles in this agroecosystem. There

are notable exceptions, such as work on the boll weevil, *Anthonomus grandis grandis* Boheman, by R. E. McLaughlin, much of which is cited later in this chapter.

As a side-effect of the recent boll weevil eradication program in the southeastern United States, several pests such as the beet armyworm, *Spodoptera exigua* (Hübner), and southern green stink bug, *Nezara viridula* (L.), among others, are becoming increasingly important in cotton. Several pathogens of the beet armyworm have been noted by the authors in cotton in Alabama and South Carolina during the 1988 field season (unpublished data). It is likely that reports will be forthcoming on pathogens of stinkbugs and similar "new" pests as they demand more attention by field entomologists working with this crop.

The reader should keep in mind that this chapter contains information on relationships that result principally from naturally occurring pathogens. Although information on the biology of several pathogens commonly used as microbial insecticides will be presented, this chapter will not review applied microbial control knowledge. This subject is covered more thoroughly in Chapter 15.

VIRAL PATHOGENS

Viruses are, in themselves, incomplete forms of life. They contain DNA or RNA that has sufficient genetic coding information to cause specific host cells to produce specific products that the cell would not normally produce, thereby causing infection. These products include viral proteins, specific enzymes, new viral nucleic acid, etc. The virus is able to direct the infected cell to produce these products at the expense of energy and material normally channeled toward growth and maintenance of the cell itself. The end result is often destruction of the cell. If sufficient cells are involved, host growth and development may be reduced or abnormal, with death being a frequent result. There are many different families of viruses that infect insects. Only five—Baculoviridae, Reoviridae, Iridoviridae, Ascoviridae, and Polydnaviridae—will be discussed as those best known from insects affecting cotton.

BACULOVIRUSES

Baculoviruses are very numerous within the Phylum Arthropoda, but the majority are known from insects. Several insect orders contain known hosts, but they are recorded principally from the Lepidoptera (Bilimoria, 1986). There are no known counterparts of this group of viruses within the plant kingdom or within the Phylum Vertebrata. The International Committee on Virus Nomenclature places these viruses in the family Baculoviridae (Matthews, 1982). Only one genus, *Baculovirus*, has been described, but there are three subgroups—A, B, and C. The latter are based on the presence or absence of a proteinaceous occlusion body which surrounds the infectious virions and, if present, on the morphology of the occlusion body. In subgroup A, commonly referred to as the nuclear polyhedrosis viruses, many virions are occluded in a polyhedral shaped occlusion body (Figures 1, 2) which forms in the host cell nucleus. In Subgroup B, a single virion is occluded in a small, capsule-shaped occlusion body (Figure 3).

Subgroup C virions are naked and do not produce any type of protective occlusion body. There are currently no known Subgroup C viruses from cotton pests.

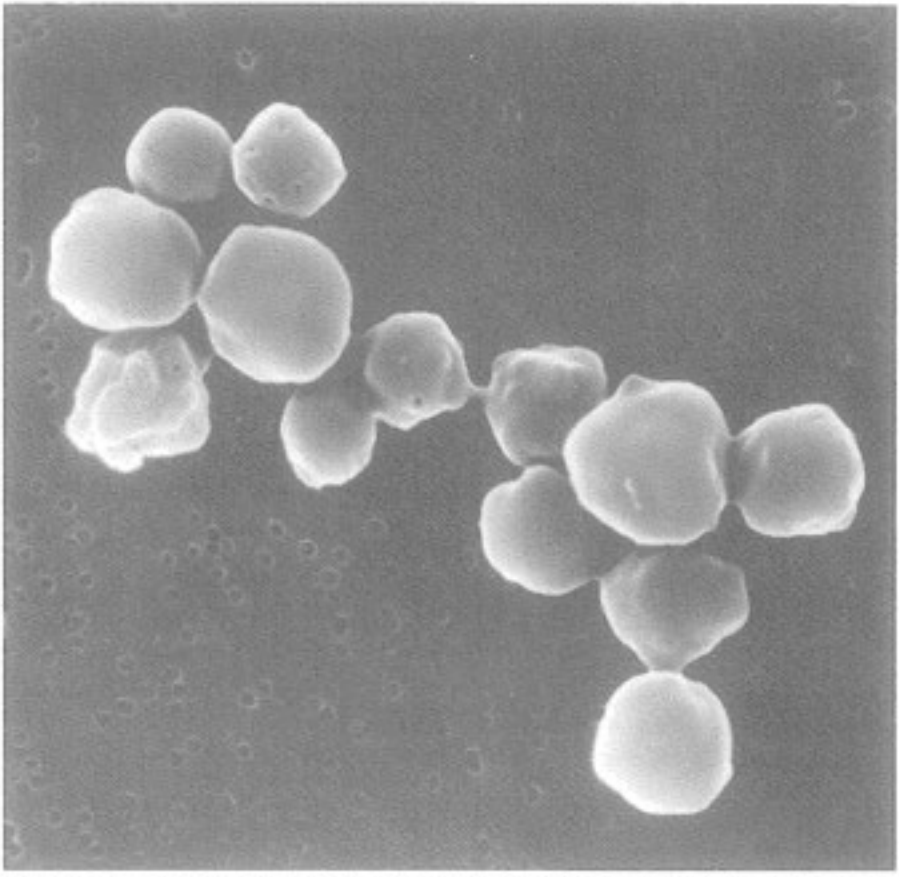

Figure 1. Polyhedral occlusion bodies of *Baculovirus* Subgroup A from infected bollworm larvae. (SEM, 7480X.)

Nuclear Polyhedrosis Virus (*Baculovirus* Subgroup A) — The nuclear polyhedrosis viruses are currently known from over 500 different hosts, mostly Lepidoptera, but also from Coleoptera, Diptera, Hymenoptera and several other orders. Within the Lepidoptera, at least 34 families contain known hosts of the nuclear polyhedrosis viruses (Martignoni and Iwai 1986). Cotton pests from which nuclear polyhedrosis viruses have been isolated include the tobacco budworm, *Heliothis virescens* (F.), the bollworm, *Helicoverpa zea* (Boddie), the beet armyworm, the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), the cabbage looper, *Trichoplusia ni* (Hübner), the cotton leafworm, *Alabama argillacea* (Hübner), the pink bollworm, *Pectinophora gossypiella* (Saunders), most of the cutworms and numerous other Lepidoptera which

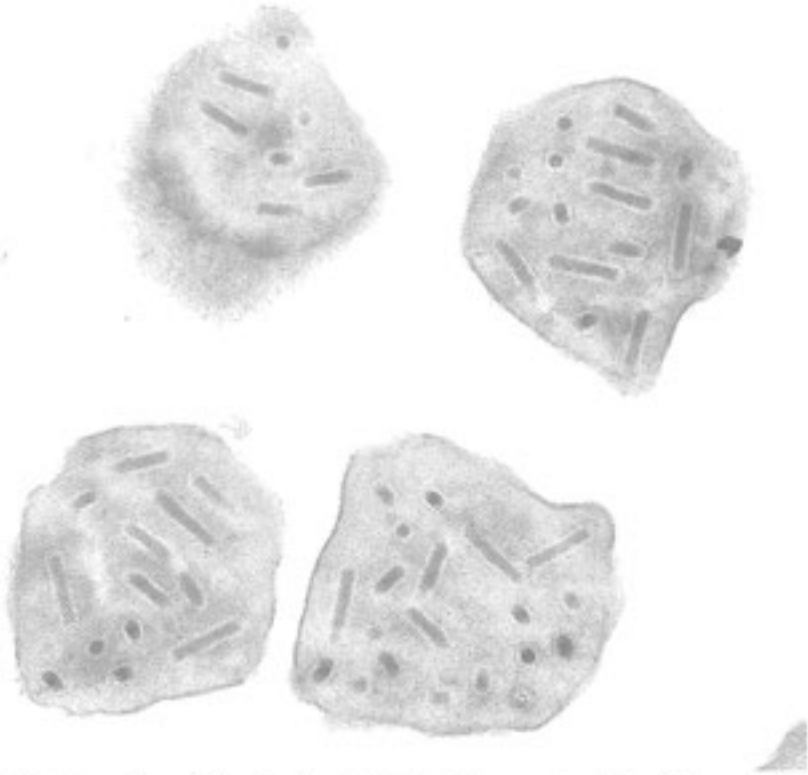

Figure 2. Cross-section of *Baculovirus heliothis* Subgroup A polyhedral occlusion bodies showing embedded virions in transverse and longitudinal sections. (TEM, 25,000X.)

occasionally attack cotton, such as the European corn borer *Pyrausta nubilalis* (Hübner), the saltmarsh caterpillar, *Estigmene acrea* (Drury), the yellowstriped armyworm, *Spodoptera ornithogalli* (Guenée) and others. Outside the United States, many other species could be added to this list.

The virions of baculoviruses, regardless of subgroup, are morphologically similar. The basic virus particle is rod-shaped and consists of a dark, electron-dense core which contains the double stranded DNA-protein complex. This is surrounded by several layers. From inside out the order is: the capsid, an intermediate layer and three outer layers collectively making up the virion envelope (Figure 3) (Federici, 1986). The nucleoprotein core plus capsid are collectively termed the nucleocapsid. Nuclear polyhedrosis virus virions are occluded or embedded in polyhedral shaped occlusion bodies (Figure 1). Occluded virions may be singly-embedded with only one nucleocapsid per envelope (Figure 2), or multiply-embedded, with two or more nucleocapsids per envelope (Figure 4). The occlusion bodies are large, predominantly from 3 to 8 hun-

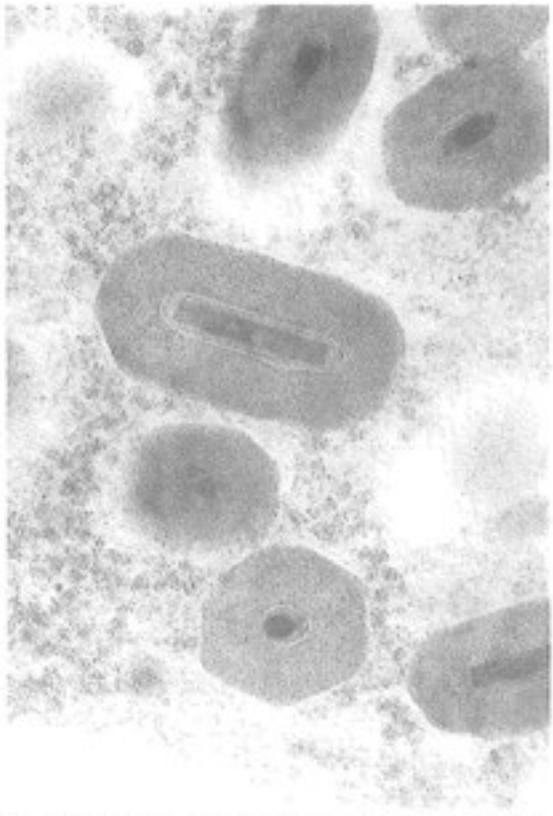

Figure 3. Cross-section of typical capsule-shaped *Baculovirus* Subgroup B occlusion bodies showing the singly-embedded virion consisting of a dense nucleo-protein core and surrounding membrane layers. (TEM, 85,000X.)

dred-thousandths of an inch (0.8 to 2.0 nanometers) in diameter, although a total size range of 2 to 60 hundred-thousandths of an inch (0.5 to 15 nanometers) is generally reported (Federici, 1986). Their size allows them to be readily seen with the light microscope. The occlusion bodies of lepidopteran nuclear polyhedrosis viruses are polyhedral in shape, being either tetrahedral, cuboidal or dodecahedral (Bergold, 1963). Viewed in profile in the light microscope, they may appear triangular, square or roughly circular, respectively. Each isolate produces a characteristic polyhedron type that is presumably genetically controlled. Each of the large occlusion bodies or polyhedra may contain from a few to several hundred occluded virions. Finally, a thin polyhedral membrane surrounds the entire polyhedron (Federici, 1986). The majority of the complete polyhedron consists of proteins. However, the virion envelopes contain

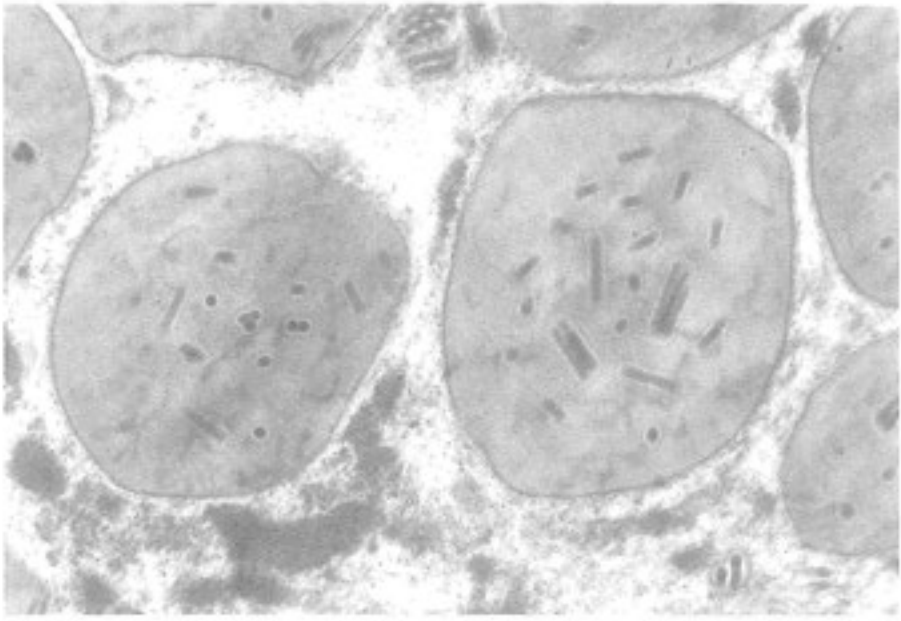

Figure 4. Cross-section of typical polyhedra from *Baculovirus* Subgroup A showing multiple-embedded nucleocapsids. (TEM, 66,500X.)

some lipid and the outer polyhedral membrane is composed principally of carbohydrates (Bilimoria, 1986; Federici, 1986).

All components of the complete polyhedron are functional and play important roles in the life of the virus. The process of infection and replication has been described well by Granados and Williams (1986). Infection is normally initiated when a susceptible insect—for example, a larval bollworm—ingests polyhedra. When the polyhedra reach the midgut, they are rapidly dissolved by the alkaline pH conditions encountered in the gut fluids, and the virions are liberated. Those which come in contact with the gut wall are taken into the cells through a process resembling phagocytosis. The envelope is lost in the process, and only the nucleocapsid enters the cell. This may enter the gut cell nucleus where the DNA is released and is able to replicate itself and produce more nucleocapsids.

Many of these newly produced nucleocapsids, as well as some of the original invaders, will eventually pass to the body cavity side of the gut cell. Via a process that is essentially the reverse of that by which they entered the gut wall cell, they will exit into the lumen of the body, picking up a new coat or envelope of cell wall material in the process. Once in the body cavity, the circulating hemolymph or blood carries the particles until they come in contact with susceptible cells. There they attach and again enter the cells by losing their temporary envelope. They finally reach the cell nucleus where the DNA is liberated and begins replicating (Granados and Williams, 1986).

Virions produced in these tissues are normally occluded into polyhedra which form within the nucleus as the virions are being produced. Occluded virions will not become active again unless ingested and released in a new host. Ultimately, an infected nucleus becomes so filled with polyhedra that it becomes distended and ruptures, releasing polyhedra into the insect's body cavity. Since tens of thousands of cells are infected, death usually occurs just before the time of multiple cell lysis (disintegration). Tissues most commonly infected include the fat body, trachea, integument and certain hemocytes. Other tissues may be involved, depending on the particular host-virus system (Smith, 1976; Granados and Williams, 1986).

The above process is the most commonly encountered. It can have certain variations. For example, the entire replication and polyhedron development process can be confined to the midgut cells with no penetration into the hemocoel and no infection of integument or internal tissues. This condition is seen in sawfly larvae (Order Hymenoptera) (Bird and Whalen, 1953; Smith, 1976) but is not known in any cotton pests. Virions can infect by being injected into the hemocoel through the integument. This occurs through feeding punctures of predators or stings of parasitic wasps that have become contaminated during similar activities on infected individuals (Andreadis, 1987). In these cases, involvement of the polyhedron in the infection process is bypassed.

Following ingestion of a lethal dosage of polyhedra, an infected larva will behave normally for several days or longer. Smaller larvae show symptoms much more rapidly than larger larvae. Time of development of disease and thus time to onset of symptoms is positively correlated with increasing temperature (Hall, 1963) and dosage. Initial symptoms include reduction in movement followed or accompanied by a loss of feeding activity. Shortly before death, the body lightens in color as billions of polyhedra form in the tissues (Figure 5). Many species of virus-infected caterpillars will move upward on the host plants. Just prior to death they attach to the plant by their terminal prolegs. They may then die laying on the leaf surface or may hang head down, attached only by the prolegs (Figure 6). Just prior to death and progressing rapidly following death, the integument (exoskeleton) becomes extremely fragile as the heavily infected cells begin to lyse (disintegrate). A progressive darkening also occurs during this same period until the larva becomes dark chocolate-brown to black (Figure 7). At this point, gently shaking or lightly touching the cadaver results in rupturing the integument and spilling the liquified body contents onto the leaf surface. Frequently, the cadaver dies in place, ruptures, and leaves a large black residue on the leaf surface which remains until washed off by rains.

The nuclear polyhedrosis viruses of cotton pests occur naturally. Infection, especially the occurrence of epizootics or increases in numbers of infected insects above a normal level, are dependent on a number of factors. These factors include presence and susceptibility of host, environmental suitability, and presence of the viable pathogen (Weiser, 1987). In addition, mechanisms of transmission are needed to facilitate infection leading to the development of epizootics (Andreadis, 1987). Nuclear polyhedrosis viruses of Lepidoptera are relatively host specific and principally infect the

Figure 5. *Baculovirus*-infected (light) and uninfected (dark) larvae of the bollworm on soybean leaves.

larval stages of their hosts. In cotton, mechanisms are needed to facilitate virus survival between host generations within and between seasons. For a given field, this could mean several years if the host insect does not reinfest the crop each year or if the field is rotated into a crop that is not attacked by a particular pest.

Nuclear polyhedrosis viruses can survive for long periods in the soil. New hosts can be infected by consuming the virus particles from previously disintegrated hosts through soil particles splashed on plants during rains or as wind-blown dust deposited on the plant (Thompson and Steinhaus, 1950). Some female moths, sublethally infected as larvae, can carry virus which contaminates the surface of their eggs as they are laid. Larvae hatching from these eggs may become infected when they eat the egg chorion. Once a small number of individuals in a population is infected, transmission is facilitated by the increased inoculum released by the disintegrating infected individuals. Predators and parasites add to the transmission level (Thompson and Steinhaus, 1950; Andreadis, 1987). Weakened, infected individuals are even cannibal-

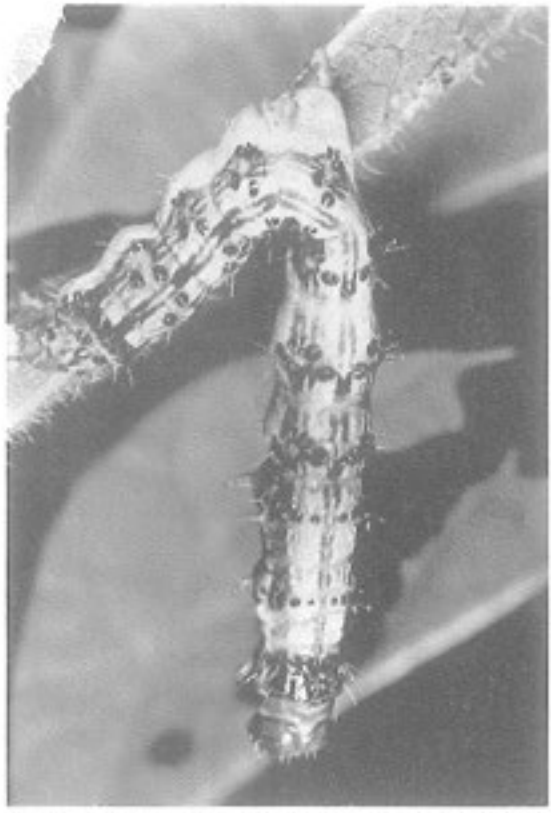

Figure 6. Bollworm larva showing typical hanging posture soon after death from *Baculovirus heliothis* infection.

ized by their healthy cohorts, which in turn are infected. An individual infected larva can produce sufficient virus to kill thousands of insects of its own kind. In an epizootic (epidemic) involving 10,000 larvae per acre or more, the amount of inoculum in a cotton field assures that most larvae will come in contact with the virus.

Environmental factors often reduce inoculum levels. Rain redistributes polyhedra on plant surfaces and spreads them more uniformly, but heavy rain-fall will wash them to the soil. Virus is rapidly inactivated by exposure to certain ultraviolet wavelengths of sunlight. Non-susceptible insects can eat virus on plants and remove it as inoculum for susceptible insects. Thus while virus builds up in the field during an epizootic, it is constantly being lost as well.

Several baculoviruses are frequently encountered in cotton fields. In the Southeast, the cabbage looper suffers routinely from epizootics of a nuclear polyhedrosis virus. Most growers are familiar with this virus-host relationship and have learned to take advantage of the natural mortality provided by this virus. Most other hosts do not show

Figure 7. Bollworm larva several hours after death caused by *Baculovirus heliothis* infection. Note darkened color and swollen body due to liquification of internal tissues and weakening of integument.

the extreme incidence of natural infection noted in the cabbage looper. An exception is the beet armyworm. This pest reached outbreak proportions in many counties of Alabama and South Carolina in 1988. Epizootics of nuclear polyhedrosis virus developed in most infested fields during late July and early August (Carner, unpublished data; Smith *et al.*, 1989).

Fruit feeding insects, while susceptible, rarely suffer from epizootics. The bollworm and tobacco budworm populations are both susceptible to a common nuclear polyhedrosis virus, but epizootics are rarely reported, despite the fact that epizootics of the virus occur in nearby peanut, soybean and corn fields. This situation appears to be related in part to the cryptic (concealed) feeding habits of the insect larvae on cotton and in part to a virus inactivating factor or factors in the cotton plant. Further research is needed to clarify this interrelationship as it has important implications not only for

the natural occurrence of this virus but also for its use as an applied microbial insecticide (see Chapter 15). Most of the nuclear polyhedrosis viruses known from cotton pest insects occur infrequently rather than causing dramatic epizootics. In these cases, they are of more interest for their potential development as microbial insecticides than for their natural impact on pest populations.

Granulosis Viruses (*Baculovirus* Subgroup B) — Discussion of the granulosis viruses parallels that of the nuclear polyhedrosis viruses with only a few exceptions. Morphologically, these viruses consist of a singly-enveloped virion which is identical in structure to that of the nuclear polyhedrosis viruses. This virion is occluded in an individual, capsule-shaped occlusion body (Figure 3) which is relatively small, 0.16 to 0.30 by 0.30 to 0.50 micrometers in dimensions (Federici, 1986). Thus they are the size of very small bacteria and, while visible with the light microscope, are more difficult to diagnose than the larger nuclear polyhedrosis viruses.

Granulosis infections are not as numerous as the nuclear polyhedrosis viruses; approximately 100 have been reported (Granados and Williams, 1986). They are known only from Lepidoptera. Of the major cotton pests in the United States, they have been recorded only from the bollworm, cabbage looper, beet armyworm, fall armyworm and several species of cutworms (Martignoni and Iwai, 1986).

Granulosis virus pathology, symptomatology and epizootiology are very similar to those of the nuclear polyhedrosis viruses. Growth rate of infected larvae is slowed resulting in a prolonged developmental time, which differs from nuclear polyhedrosis virus. Certain granulosis viruses infect the integument while others do not. Host larvae infected by the latter have an integument that remains tough and leathery after death. Those granulosis viruses that do infect the integument produce a very fragile cadaver as was described for nuclear polyhedrosis virus infection (Smith, 1976).

CYTOPLASMIC POLYHEDROSIS VIRUSES

Broadly grouped in the family Reoviridae, the cytoplasmic polyhedrosis viruses have affinities with certain plant and vertebrate viruses. They are known from over 150 different insect hosts, including Diptera and Lepidoptera, but the majority are known from infections of larval Lepidoptera (Matthews 1982). Cotton pests with recorded cytoplasmic polyhedrosis virus infections are the cabbage looper, fall armyworm, beet armyworm, tobacco budworm, bollworm, pink bollworm, many of the cutworms and other armyworms (Martignoni and Iwai, 1986). Thus, they are nearly as numerous among cotton pests as are the nuclear polyhedrosis viruses. On the other hand these recorded infections were usually from insects collected on plants other than cotton.

The cytoplasmic polyhedrosis viruses have been known for many years because they, like the nuclear polyhedrosis viruses, produce large, light microscopically visible occlusion bodies. They differ markedly in virion morphology, however. Cytoplasmic polyhedrosis virus virions are small, subspherical icosahedra. Their diameters range from 50 to 65 nanometers and can only be viewed with the electron microscope. The virions consist of a spherical nucleoprotein core surrounded by an outer shell

(Matthews, 1982). These virions are occluded within proteinaceous polyhedra as are the baculoviruses (Figure 8). The polyhedra can also vary in shape, ranging from tetrahedrons to icosahedrons (Aruga, 1971). A morphological study of seven different cytoplasmic polyhedrosis viruses by Cunningham and Longworth (1968) provided a range of mean polyhedron diameters of 1.13 to 2.49 nanometers.

Following ingestion by susceptible host insects, the polyhedral occlusion bodies are rapidly dissolved in the guts of their hosts. The released virions attach to the midgut wall and enter the cell cytoplasm. Once in the midgut cytoplasm, replication of the nucleic acid and synthesis of all virion and polyhedral components begin. Infection is confined to the cells of the midgut (Watanabe, 1971). Mature polyhedra are released into the gut as infected cells die and may be excreted in large numbers in the frass or fecal material (Aruga, 1971; Boucias and Nordin, 1978). Ultimately, severe infection results in loss of the midgut's ability to absorb food and function properly resulting in the host's death.

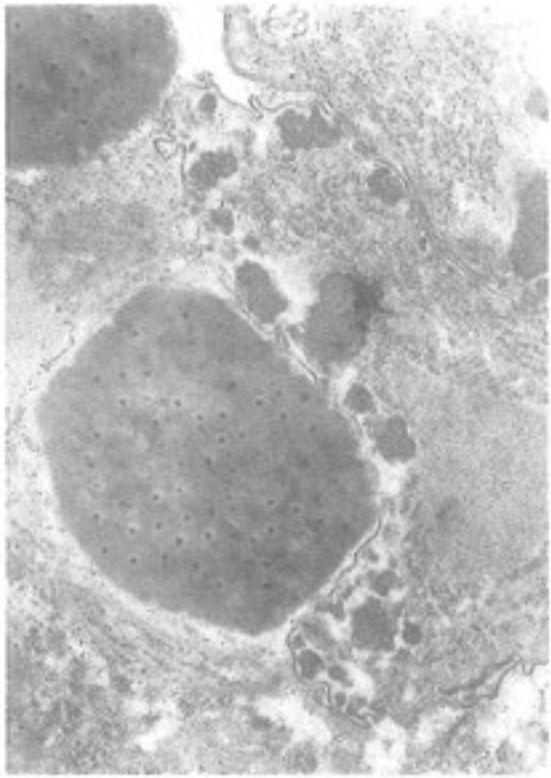

Figure 8. Thin section of midgut tissue from bollworm showing a cytoplasmic polyhedrosis virus polyhedron with many embedded icosahedral shaped virions.

Larvae infected with cytoplasmic polyhedrosis virus show few abnormal symptoms for several days after ingestion of the virus. Close examination reveals a reduction in general activity including a loss of appetite after two to four days. Larvae may regurgitate or pass abnormally wet fecal material as the infection advances. Frass also lightens in color due to presence of large numbers of occlusion bodies (Boucias and Nordin, 1978). In some host species, a white or light patchiness may appear late in infection. Dissection of the larva at an advanced stage of infection reveals a very light-colored yellow to opaque midgut instead of the normal semi-transparent tissue. This is caused by the presence of large numbers of polyhedra packing the cytoplasm of the midgut cells (Smith, 1976). At death, the larva darkens, turning brown to blackish. Unlike the nuclear polyhedrosis infection, it maintains a very tough integument which does not rupture when touched. Larvae infected late in their development often survive, pupate and emerge as adults.

Most virus is transmitted when healthy larvae eat foliage that has been contaminated by fecal material or regurgitate of infected larvae. The virus can also be transmitted from infected females to their offspring as a contaminant on the egg surface which is ingested by newly-hatched larvae. Sublethally infected female larvae that pupate and successfully emerge as moths can carry virus through metamorphosis. The virus then contaminates eggs as they are laid. In the tobacco budworm this mode of transmission occurred even after diapause was complete (Sikorowski *et al.*, 1973).

IRIDOVIRUSES

Iridoviruses are large, icosahedral, DNA viruses belonging to the family Iridoviridae. Those isolated from insects are grouped into two genera based on their sizes and serological relationships. The smaller iridescent viruses (about 130 nanometers) have been placed in the genus *Iridovirus* and include isolates from Diptera (Tipulidae), Coleoptera and Lepidoptera. Larger iridescent viruses (about 180 nanometers) have been isolated from mosquitoes and other Diptera. They are placed in the genus *Chloriridovirus* (Hall, 1985).

The name Iridoviridae is based on the characteristic iridescent green, blue or purple seen in heavily infected hosts, which is caused by the presence of high concentrations of the virus packed in crystalline arrays (Figure 9). The iridoviruses replicate in the cytoplasm of cells in a wide range of tissues, but heaviest concentrations are usually found in the fat body. There are two reports of these viruses infecting *Helicoverpa/Heliothis*. Carey *et al.* (1978) isolated a small iridescent virus (about 130 nanometers) from *Helicoverpa armigera* (Hübner) in Africa, and Stadlebacher *et al.* (1978) recovered a similar virus from bollworm larvae collected from clover and vetch in Mississippi. Infected bollworm larvae turned an iridescent lavender-blue, blue, or blue-green. The virus from the bollworm ranged in size from 131 to 160 nanometers with an average diameter of 145 nanometers. Therefore, both the Africa and United States isolates probably belong to the genus *Iridovirus*.

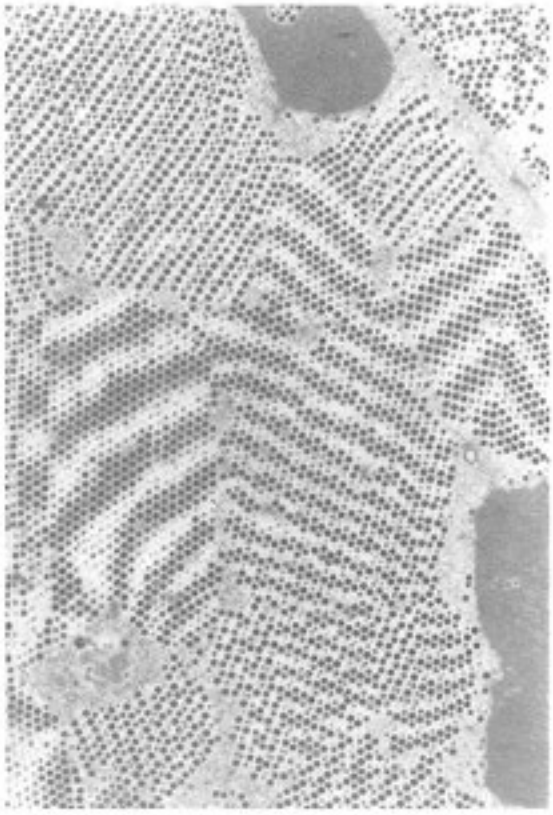

Figure 9. Thin section of fat body cells with virions arranged in the crystalline array pattern typical of *Iridovirus* infection. (TEM, 7,400X.)

ASCOVIRUSES

Ascoviruses are a recently discovered group of viruses which have been isolated from several species of noctuid larvae. They are non-occluded, enveloped, DNA viruses that measure 150 by 400 nanometers. Federici (1983) proposed the name Ascovirus to describe the many virus-containing vesicles found in the hemolymph of infected larvae (Figures 10 and 11). The virus was first reported from bollworm/tobacco budworm larvae in Mississippi (Adams *et al.*, 1979) and South Carolina (Carner and Hudson, 1981). Similar viruses have been reported from the cabbage looper (Federici, 1983) and the fall armyworm (Hamm *et al.*, 1986). Symptoms in infected larvae include sluggishness, reduced feeding and stunted growth. Larvae may remain alive for several weeks after infection. As the disease progresses the

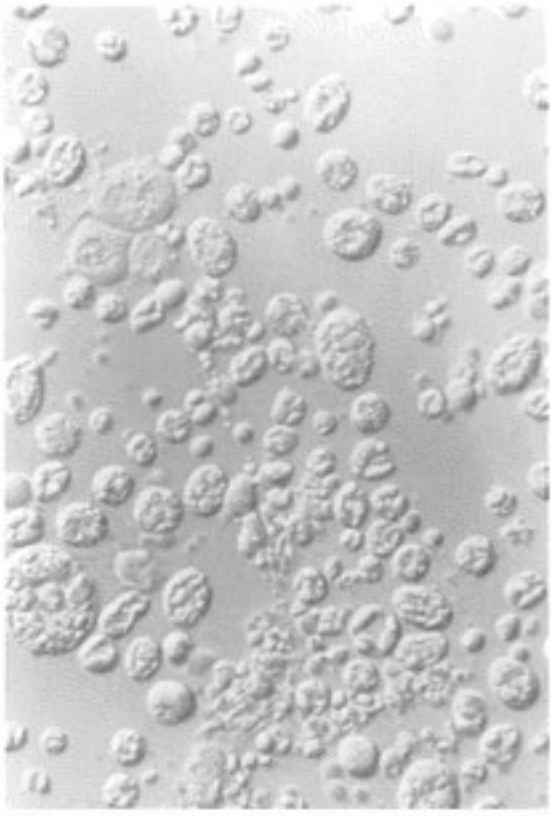

Figure 10. Hemolymph from a bollworm larva with Ascovirus infection. Note the large number of vesicles that are granular in appearance due to the presence of clumps of virus particles. (Nomarski interference contrast, 1000X.)

hemolymph turns milky and becomes filled with virus-containing vesicles. The vesicles are formed by a unique developmental sequence in which the host cell cleaves into a cluster of vesicles as virus formation progresses. The host cell then ruptures, releasing the vesicles into the blood or hemolymph.

The virion is allantoid in shape and consists of a DNA/protein core of similar shape surrounded consecutively by an inner membrane and an outer envelope (Figure 11). The external surface of the inner membrane and the outer envelope have a reticulate appearance in negatively stained preparations. Replication is initiated in the nucleus, but virion assembly does not occur until after disruption of the nuclear envelope. Subsequently, host cells are cleaved into vesicles in which replication and assembly appear to continue. Ascoviruses vary in their tissue specificity. The isolate from boll-

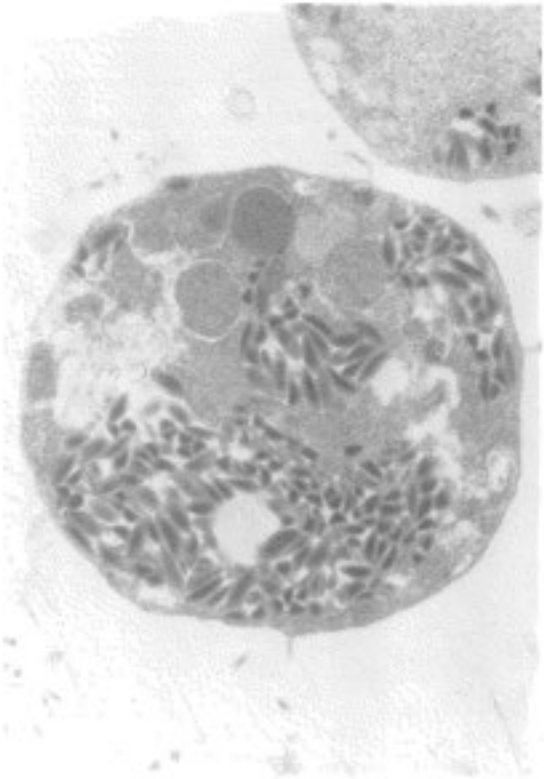

Figure 11. Thin section of a single vesicle from hemolymph of Ascovirus-infected bollworm larva. Note clumps of dark-stained virions. (TEM, 23,000X.)

worm/tobacco budworm and the cabbage looper replicates primarily in epidermal and fat body cells. It has also been observed in tracheal matrix and midgut epithelium. The isolate from *Spodoptera* spp. is restricted primarily to the fat body.

In some cotton fields in South Carolina, infection levels in bollworm/ tobacco budworm populations have reached 20 to 30 percent, but usually levels are much lower. Field collections have shown that infection levels are usually higher in fields where parasitoid populations are high, leading one to believe that virus transmission is mediated by parasites. Hamm *et al.* (1985) demonstrated that the braconid parasite, *Cotesia marginiventris* (Cresson), could transmit the virus between larvae of the fall armyworm. In South Carolina, the parasite, *Microplitis demolitor* (Wilkinson), was used successfully to transmit the virus between bollworm larvae (Carner, unpublished data). In the laboratory it is difficult to transmit the virus to larvae by feeding. However,

piercing the cuticle of larvae with a contaminated pin usually results in 100 percent infection, presenting more evidence that parasites may play an important role in the transmission of this virus in the field. In both cases of parasite transmission the virus killed not only the host larva, but also the developing parasite, putting in question the beneficial nature of this virus.

POLYDNAVIRUSES

Polydnavirus is the name used by researchers to refer to a unique group of nonoccluded viruses found in the ovaries of parasitic wasps. The name was derived from the characteristic multi-segmented DNA of variable molecular weight found in all of these viruses. Morphologically, these viruses can be divided into two main groups. Those found in braconid wasps such as *Cardiochiles nigriceps* (Viereck) consist of a short rod-shaped nucleocapsid surrounded by a double envelope. They are very similar to some of the nonoccluded baculoviruses and were originally classified by some researchers as a subgroup of the Baculoviridae (Stoltz and Vinson, 1979). Viruses found in the oviducts of ichneumonid wasps such as *Campoletis sonorensis* (Cameron) are spindle shaped and do not resemble any known group of viruses. Stoltz *et al.* (1984) proposed that these ichneumonid viruses be placed in a new family, the Polydnaviridae. Most researchers agree that eventually both the braconid and ichneumonid viruses will be grouped together in a separate family because of similar characteristics of the DNA genome.

These parasite viruses replicate in the nuclei of calyx cells and high concentrations of the virus accumulate in the lumen, forming what is referred to as the calyx fluid (Figure 12). This fluid is injected into the hemolymph of the host at the time of oviposition. The major function of these injected viruses is to interfere with the immune system of the host and prevent encapsulation of the parasite egg (Edson *et al.*, 1981). Some viruses also prevent development of the host by affecting hormone levels, and thus make the host more suitable for development of the parasite (Dover *et al.*, 1988). Each parasite species possesses a virus which is unique for that species, and the virus is present in all female individuals of that species.

Many of the viruses described to date have been from parasites which affect cotton insect pests. These include the braconids: *Cardiochiles nigriceps* Viereck, *Microplitis croceipes* (Cresson) and *Cotesia marginiventris*; and the ichneumonid, *Campoletis sonorensis* (Stoltz and Vinson, 1979). It is likely that most, if not all, of the braconid and ichneumonid parasites found in cotton possess a calyx virus characteristic for their family.

FUNGAL PATHOGENS

The fungal pathogens of insects are unique in that they are able to invade their hosts by penetration through the integument. Every major pest of cotton in the United States is infected by at least one known fungal pathogen; most are infected by several. Insects which feed by piercing and sucking, e.g. aphids, whiteflies, thrips, spider mites and

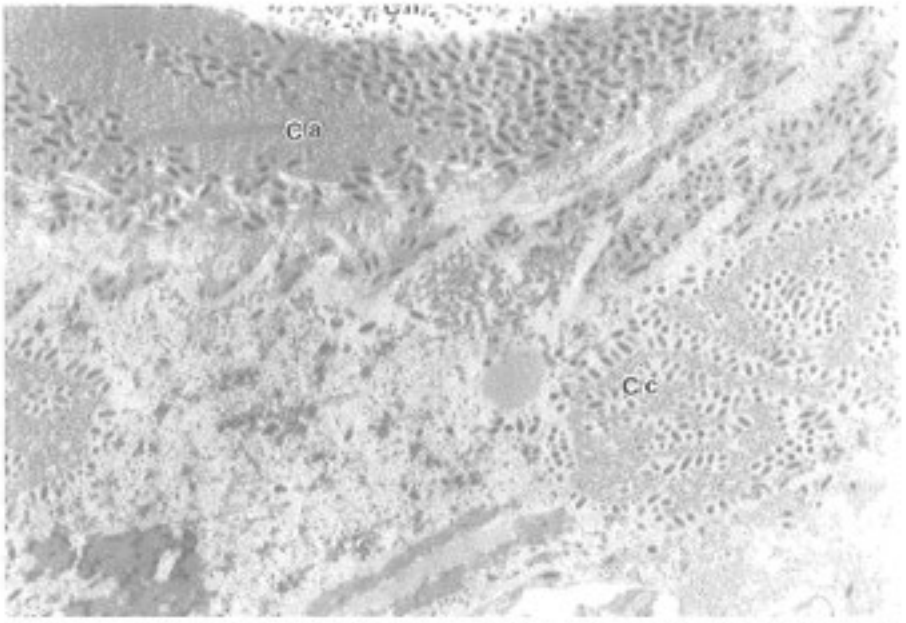

Figure 12. Thin section from the calyx region of an oviduct from the parasite *Campoletis sonorensis* showing Polydnavirus virions in the calyx fluid (Ca) which is adjacent to the chorion (Ch) of an egg. Virus replication is taking place in the calyx cell (Cc). (TEM, 10,500X.)

stinkbugs rarely are reported to have pathogenic infections of bacteria, viruses, or protozoa since ingestion of inoculum would be rare. Fungal infections are recorded in each of these groups, and dense populations frequently support striking epizootics (epidemics). Factors favoring epizootics of entomopathogenic fungi are both biotic and abiotic. Fungi are dependent on host density and on specific climatic factors such as wind, humidity, temperature, light and others to initiate and maintain infection in a host insect. Epizootics are dependent on these same factors plus various host population parameters such as density, age structure, distribution within fields and seasonal occurrence or distribution. Initiation and maintenance of epizootics are thus dependent on many specific conditions.

The canopy of the cotton plant provides an ideal situation for the development of fungi, especially in fields where the canopy is closed between rows. Late season populations of insects and mites are usually infected by one or more species of fungal pathogens. Because of the dependence of fungal pathogens on favorable moisture conditions, incidence of these pathogens in pest populations may vary considerably from one season to the next. Most of the studies dealing with fungal pathogens of cotton insects are concerned with natural occurrence and epizootiology of these pathogens. There has been very little work on development of these pathogens as microbial insecticides.

Fungal pathogens reported from cotton insects and mites fall into two main groups: those belonging to the order Entomophthorales and those which are members of the imperfect fungi.

ENTOMOPHTHORALES

The order Entomophthorales is made up of a large group of highly specialized fungi in the class Zygomycetes which are mainly parasitic on insects and arachnids (mites and spiders). The classification of this group has been the subject of considerable controversy in recent years. Early reports placed most species in a single genus, *Entomophthora*. However, as new species were added to the group and the number of species in the genus exceeded 100, attempts were made to develop a more manageable system of classification. Several revisions of the group have been published including those by Batko (1964), Remaudiere and Keller (1980), and Humber (1989). For this chapter we will use Humber's classification which divides the order into six families and 21 genera. Representatives of this group which are found in cotton include the genera *Erynia*, *Pandora*, and *Entomophaga* in the family Entomophthoraceae and *Neozygites* in the family Neozygitaceae.

The vegetative phase of the Entomophthorales fungi occurs within the body of the live host, usually in the form of hyphal bodies. These increase rapidly by fission or budding, completely filling the hemocoel and killing the host. Shortly after the death of the host, conidiophores grow out from the hyphal bodies and emerge through the less resistant portions of the cuticle. In some cases the conidiophores will form a mat which completely covers the body of the host (Figure 13). Conidia are formed singly on the tips of the conidiophores and are forcibly ejected from the host cadaver. The spores have a sticky coating and will adhere to any substrate with which they come in contact. The aureole or opaque circle of ejected conidia usually seen around a host cadaver is a diagnostic characteristic for this group of fungi.

The conidia are the primary infective units which spread the fungus through a population. In some species the primary conidia serve this purpose. In other species specialized secondary conidia are formed at the tips of slender vertical stalks. Hosts become infected by walking over the leaf surface and brushing against these spores. Conidia can be spherical, pear-shaped, or slender, depending on the species and can vary in length from 10 to 30 micrometers (Figure 14a, b, c).

Most species of Entomophthorales also form thick-walled resting spores (Figure 15) which aid in the survival of the fungus during harsh conditions and when hosts are not present. These spores are formed inside the host, often in individuals other than those on which conidia are formed. Hosts containing resting spores usually will display symptoms completely different from those infected with the conidial stage of the fungus.

Carner *et al.* (1975) reported a species of Entomophthorales with pear-shaped conidia (Figure 14b) infecting larvae of the bollworm in soybeans in South Carolina. Hamm (1980) found a similar species infecting bollworm/tobacco budworm larvae in sorghum and identified it as *Entomophthora aulicae*. Both reports describe what is now known as *Entomophaga aulicae* (Reichardt) Humber (Humber, 1989). This same

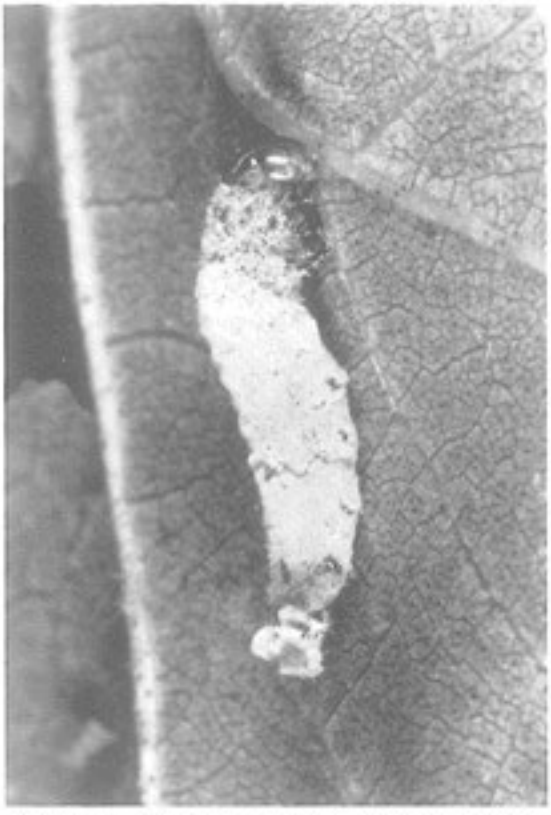

Figure 13. Bollworm larva killed from infection by *Erynia* sp. The cadaver is covered with a dense mat of hyphae and sporulating conidiphores.

fungus has been observed infecting bollworm/ tobacco budworm larvae in late-season cotton in South Carolina. The fungus usually infects late instar larvae and produces large pear-shaped conidia which contain 10 to 12 nuclei (Figure 14b). Bollworm/ tobacco budworm larvae in these same populations were also infected by a different species of Entomophthorales, which infected smaller larvae (mainly 2nd and 3rd instars) and differed from *Entomophaga aulicae* in that it produced an extensive mycelial mat over the exterior of the larval cadaver. Conidia were also smaller, more fusiform (spindle-shaped) than pyriform (pear-shaped), and contained only one nucleus per spore (Figure 14a). This second fungus is probably a species of *Erynia*.

The predominant species of looper on cotton is the cabbage looper. However, populations of the soybean looper, *Pseudoplusia includens* (Walker), sometimes build up in late-season cotton. Both species can be infected by *Pandora gammae* (Weiser) Humber, a fungus which plays a significant role in reducing looper populations in soybeans (Harper and Carner, 1973). In cotton this fungus is usually found in late season

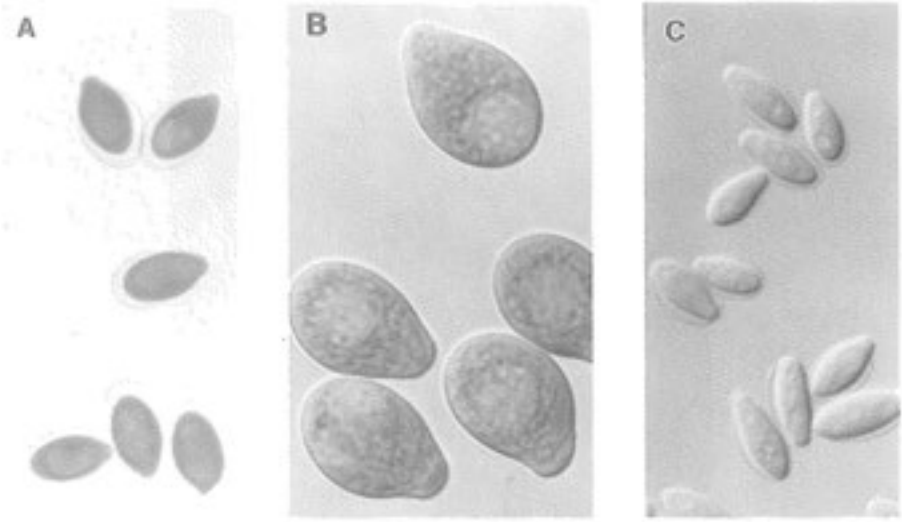

Figure 14. Conidia from the different genera of Entomophthorales. A. *Erynia* sp. from bollworm (800X). B. *Entomophaga aulicae* from bollworm (1,000X). C. *Pandora gammae* from soybean looper (1,100X).

populations which are predominantly soybean looper. Loopers infected with *Pandora gammae* display different symptoms depending on the type of spore produced. Larvae infected with the conidial stage are completely covered with a mat of tan-colored conidiophores (Figure 16). After conidia (Figure 14C) are produced, larvae turn brown and become shriveled. Larvae infected with the resting spore stage of the same fungus are black and swollen and have no external growth (Figure 17). Unidentified species of *Erynia* and *Entomophaga* have also been seen infecting loopers in cotton (Carner, unpublished). These fungi produce symptoms similar to those described in bollworm/tobacco budworm larvae.

The beet armyworm has been a serious pest of cotton in recent years. Although the nuclear polyhedrosis virus has usually been reported as the predominant pathogen of this species, a species of *Erynia* has also caused high mortality in populations of this pest in South Carolina. This *Erynia* spp. appears similar to the one which infects bollworm/tobacco budworm larvae. The yellow-striped armyworm is also a host for this fungus. Both the yellowstriped and beet armyworms have been found infected with *Pandora gammae* (Carner, unpublished).

The cotton aphid, *Aphis gossypii* Glover, has become increasingly important as a pest of cotton in the southeastern United States during the past decade. The fungus *Neozygites fresenii* (Nowakowski) Batko is a common mortality agent of this pest in many states in most years. Dramatic epizootics or outbreaks of the fungus are frequently observed, with high percentages of population reductions. The authors have noted these in Alabama and South Carolina and reports from other states have been common (Steinkraus, 1991).

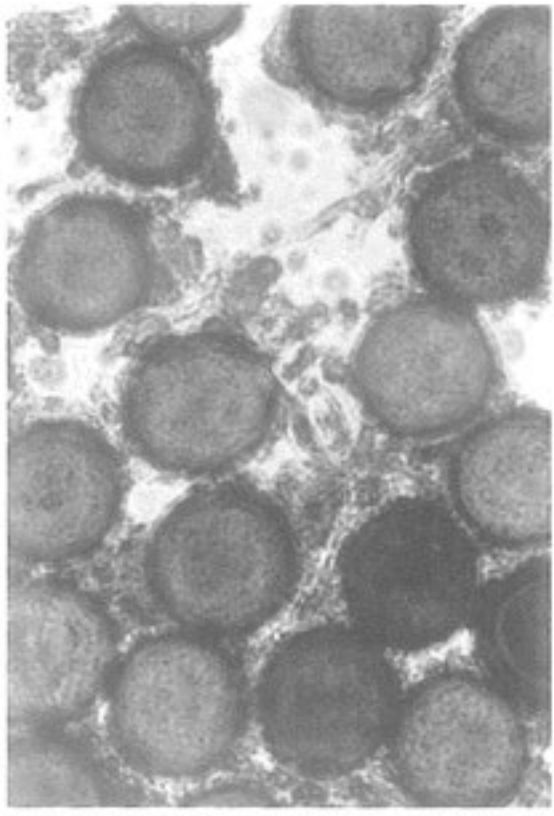

Figure 15. Resting spores of *Neozygites floridana* from the twospotted spider mite. (1370X.)

The predominant mortality factor in populations of the twospotted spider mite, *Tetranychus urticae* (Koch), is the fungal pathogen, *Neozygites floridana* (Weiser) Remaudiere and Keller (Figure 18). Epizootics of this fungus usually occur when mite populations reach high levels and can completely decimate populations within a period of one to two weeks (Carner and Canerday, 1970). Mites infected with the conidial stage of *Neozygites floridana* become mummified and turn a light tan color immediately after death. Under high humidity conditions conidiophores and conidia will develop over the entire external surface. Primary conidia are spherical with a prominent papillar base and contain four nuclei. The infective stage of this fungus appears to be a specialized secondary spore which is produced at the tip of a slender vertical stalk which grows out from the primary conidium (Figure 19). Mites infected with the resting spore stage of this fungus are black with no external growth (Carner, 1976).

Populations of the western flower thrips, *Frankliniella occidentalis* (Pergande), are sometimes infected with the fungal pathogen, *Neozygites parvispora* (MacLeod and Karl) Remaudiere and Keller, a species originally described from the onion thrips,

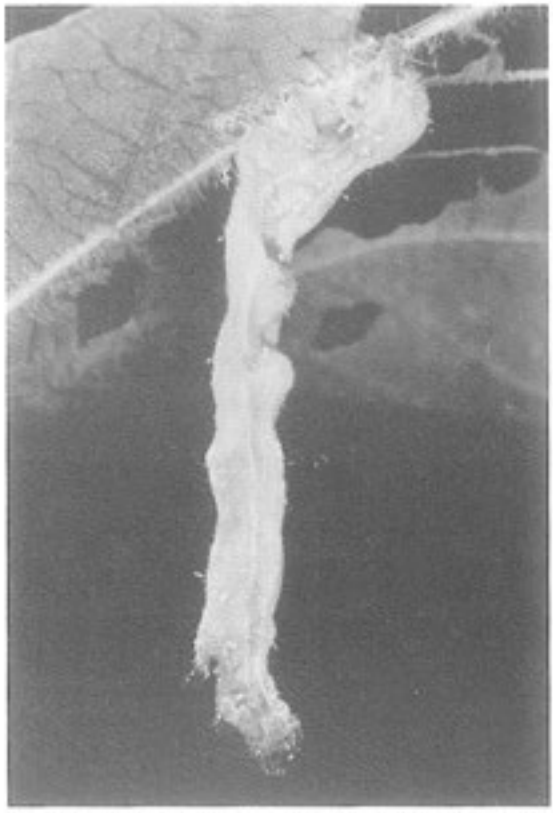

Figure 16. Soybean looper larva hanging from a soybean leaf early in the morning following death the previous evening from *Pandora gammae* infection in which conidia were formed. The body is covered with a layer of tan-colored conidiophores.

Thrips tabaci (Lindeman) (Carner, unpublished). This fungus has a life cycle very similar to that described for *Neozygites floridana* in spider mites.

Members of the Entomophthorales are specialized pathogens with a high degree of adaptation to the species which they infect. They are generally observed causing epizootics when host populations are high. Like most fungi they are dependent on favorable environmental conditions for their development, but not to the extent that imperfect fungi are. These fungi are closely tied to the life cycle and behavior patterns of their hosts and can maintain infection in a population with the normal periods of high humidity that occur at night. For example, the mite fungus, *Neozygites floridana* kills its host in the late afternoon and early evening when conditions are favorable for spore production. Conidiophore production begins immediately and is completed

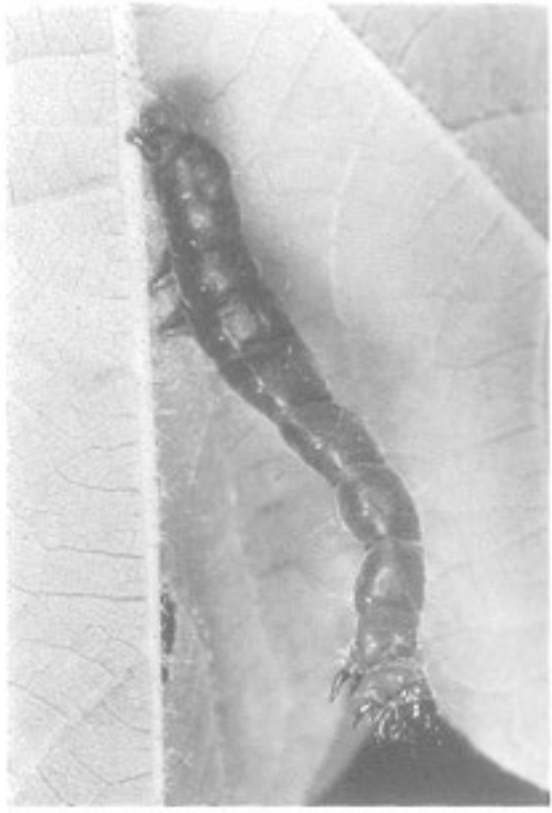

Figure 17. Soybean looper larva hanging from a cotton leaf following death from *Pandora gammae* infection in which resting spores were formed internally.

within several hours. As soon as primary conidia are ejected and land on the leaf surface, they germinate to form slender upright stalks on which secondary conidia are formed. All of this development takes place during the night while the humidity is high. The secondary spores are more resistant than the primary conidia and are able to survive the warm dry conditions that normally occur during the daylight hours. Spider mites are inactive at night and begin to move around on the leaves as temperatures rise during the morning. As they move around on the leaf surface they brush against the secondary spores and the spores become attached to the cuticle. Germination of these infective secondary conidia does not occur until conditions become favorable again the following evening. Spore germination and penetration of the cuticle requires humidities close to 100 percent, but once the fungus is inside the mite it does not require high humidity for its development until it kills the mite several days later.

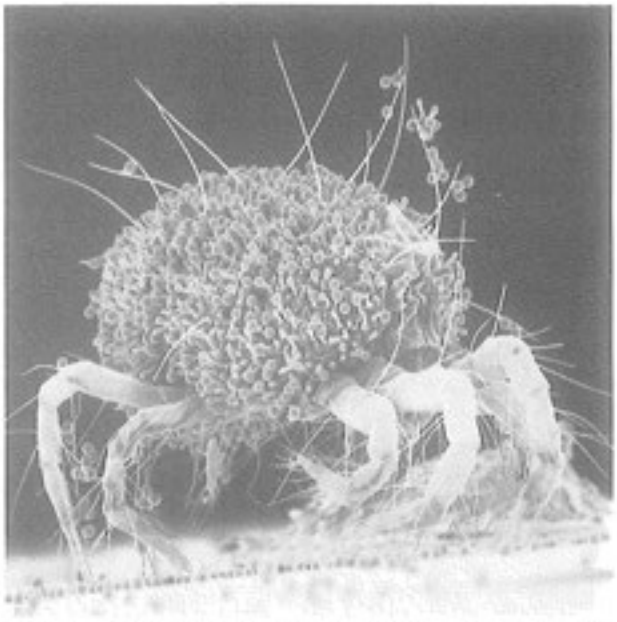

Figure 18. Twospotted spider mite infected with *Neozygites floridana* showing the formation of primary conidia. (SEM, 140X.)

NOMURAEA RILEYI

Nomuraea (Spicaria) rileyi (Farlow) Samson is a member of the class Hyphomycetes. As such it produces conidia but has no known sexual method of reproduction. There is only one other species in the genus, *Nomuraea atypicola* (Yasuda) Samson, which is distinctively different based on conidial color. It is not known to infect any cotton pests.

Nomuraea rileyi is commonly encountered as a pathogen in many species of lepidopterous larvae in cotton fields (Ignoffo, 1981). It frequently infects tobacco budworms, bollworms, cabbage loopers and the armyworms associated with cotton. On other crops—corn, sorghum, soybean, and crucifers—it is found on additional species of Lepidoptera. *Nomuraea rileyi* has been reported from most agricultural areas around the world, ranging from tropical to temperate climates (Ignoffo, 1981). Most records appear to be associated with larval noctuids, but the species is recorded from a spider (Samson, 1974) and from several Coleoptera (Ignoffo, 1981), so the potential host range may be large.

Nomuraea rileyi is very similar in morphology to *Penicillium* (Samson, 1981). It produces oval conidia which are green in color. These are produced in chains on short-necked phialids which are in turn produced in dense whorls along the filament-like conidiophores (Figure 20).

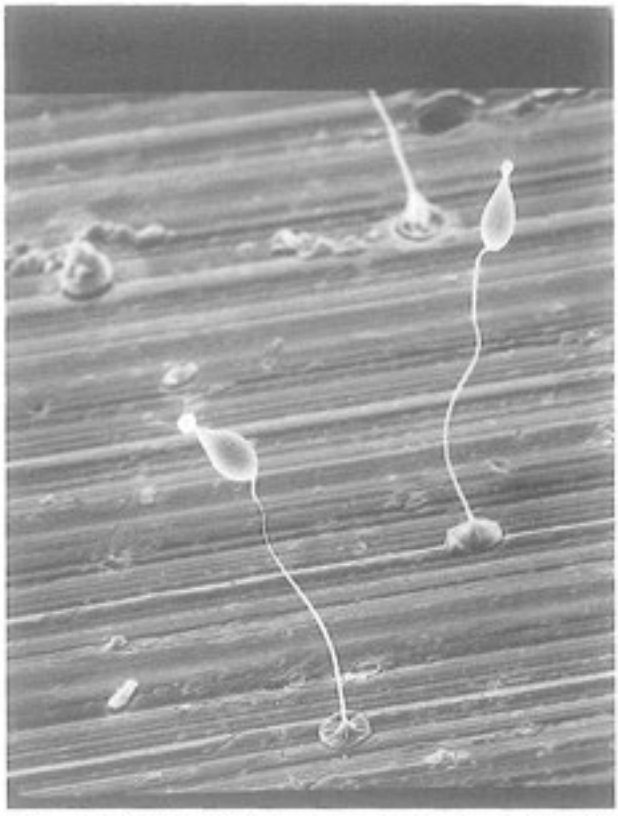

Figure 19. Capilliconidia of *Neozygites floridana*. Note the development of the capillary stalk from the primary conidium on the substrate with the subsequently formed capilliconidium and adhesive tip. (SEM, 750X.)

Insect larvae infected with *Nomuraea rileyi* exhibit symptoms typical for many Deuteromycete infections. Little external differences are noted between infected and healthy individuals for several days following infection. Larvae then become less active. Neonate cabbage looper larvae are killed in six to seven days, depending on temperature (Getzin, 1961). Following death, larvae may hang from the plant structures on which they are sitting with their prolegs attached to the plant surface. On cotton, infected bollworm or tobacco budworm larvae are sometimes seen hanging head down from their feeding holes in the bolls. On leaves and stems, the larvae often assume a curved posture, arching upward and forward from their attached prolegs with the forward portion of the body held rigidly above the substrate. If the correct environmental conditions are present, the fungal mycelium or hyphal bodies which have proliferated and filled the hemocoel of the cadaver will begin to produce conidiophores. These grow through the body wall in large numbers and ultimately cover the

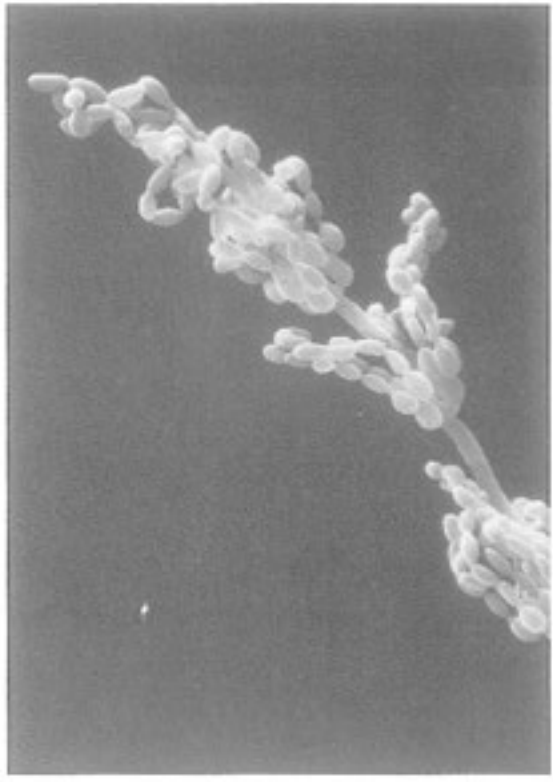

Figure 20. SEM of *Nomuraea rileyi* reproductive structures showing chains of spores produced from dense whorls of conidiogenous cells. (1,300X.)

entire cadaver as a dense, bright white bloom. It is this stage that is most frequently noticed by growers. If environmental conditions continue to be favorable, this stage is followed by the production of hundreds of thousands of green conidia which cause the cadaver to turn from bright white to a light green color (Figure 21). Touching or shaking such cadavers results in dislodging conidia as a green dust.

Infection of a larva by *Nomuraea rileyi* begins when conidia which have either adhered to the integument or have been ingested, germinate and produce germ tubes which penetrate through the integument or gut wall by both mechanical and chemical mechanisms. Once penetration occurs, the germ tube begins to produce cells beneath the integument by growth and division at the penetration site. Growth continues as cells break away and grow in the hemolymph as short, stocky hyphal bodies, often called blastospores. These proliferate by budding, eventually causing death of the host. They continue to grow until they fill the host abdomen. At this stage, they produce elongate conidiophores and conidia as discussed under symptomatology.

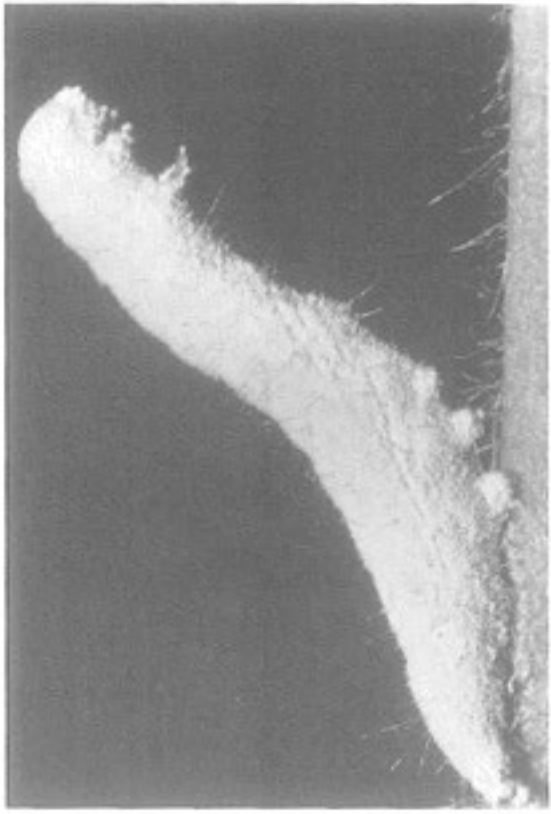

Figure 21. Typical *Nomuraea rileyi*-infected lepidopterous larva in complete sporulation stage. Larvae are light green in color at this stage.

Nomuraea rileyi is typically abundant under conditions of high humidity and high host density. In most cotton growing areas of the United States such conditions are not continuously present. Infection is frequently noted in individual larvae in low incidence during much of the growing season, but the fungus is normally prevalent in highest incidence in host populations during late summer. This is probably due to development of microclimates within the closed crop canopy conducive to fungal infection and spread, as well as to higher host populations increasing the probability of infection. Production of conidiophores and conidia from dead cadavers is dependent on moisture conditions, especially on high humidity. Once produced, conidia are easily dislodged from the cadavers by wind or other physical disturbance and contact new hosts by air movement or by gravity. If conditions for conidiophore and conidia production are not appropriate, the fungus can remain dormant inside the intact dead larva for extended periods of time. The fungus overwinters inside the host or as free conidia (Sprenkel and Brooks, 1977; Ignoffo, 1981).

BEAUVERIA BASSIANA

Beauveria bassiana (Balsamo) Vuillemin is a deuteromycete whose life cycle, epizootiology and ecology is very similar to that of *Nomuraea rileyi*. However, this fungus has a much wider host range than *Nomuraea rileyi*. It has been isolated from many different orders of insects. It, too, has been isolated from all major temperate and tropical regions of the world.

Morphologically, *Beauveria bassiana* differs from *Nomuraea rileyi* in the structure of its conidiophores (Samson, 1981). Conidia are produced along zig-zag shaped conidiophores rather than in chains (Figure 22). This configuration is very distinctive and characteristic of the genus, but requires high magnification and careful specimen preparation to be able to discern. The conidiophores resemble those of *Nomuraea rileyi* in that the conidia-bearing cells are produced in whorls along the conidiophores. *Beauveria bassiana* is also distinctive in its production of snowy white conidia which are generally produced in a layer that closely covers the cadaver. In some insects, the

Figure 22. SEM of *Beauveria bassiana* reproductive structures showing spores produced in a zig-zag pattern from single conidiogenous cells. (6,500X.)

conidia are produced in clumps over the body surface, creating a more granular appearing surface.

Beauveria bassiana has been found in nearly every major order of insects including Coleoptera, Lepidoptera, Orthoptera, Hemiptera, Homoptera, Diptera, Hymenoptera and many others. Cotton pests known to have been infected include adult boll weevils (McLaughlin, 1962; Smith, 1991), the tarnished plant bug, *Lygus lineolaris* (Paliot de Beauvois) (Unpublished data, M. J. Gaylor, Entomology Department, Auburn University, Auburn, Alabama), the western plant bug, *Lygus hesperus* (Knight) (Dunn and Mechalis, 1963), and several armyworms, *Spodoptera* spp. (Gardner and Fuxa, 1980; Kenneth and Olmert, 1973). All of these records were encountered under laboratory conditions. Naturally infected insects are rarely found in the field. Wright and Chandler (1991) recently isolated a strain of *Beauveria bassiana* from boll weevil in the Rio Grande Valley of Texas. In addition to the weevil, Wright (1992) has successfully infected the sweetpotato whitefly, *Bemesia tabaci* (Gennadius) and the cotton fleahopper, *Pseudatomoscelis seriatus* under both laboratory and field conditions. The strain is currently being developed as a potential microbial insecticide for use against these and other pests in cotton (see Chapter 15).

Infection, growth, development and sporulation of *Beauveria bassiana* is essentially as described for *Nomuraea rileyi*. Symptoms are also similar with the exception of the color of conidia produced by each. The pure white color of *Nomuraea rileyi* in the conidiophore bloom stage is similar to the color of both the conidiophore and conidial stages of infection by *Beauveria bassiana*. The two can be separated by holding them under humid conditions for conidia production or by microscopic examination of the conidiophores.

The principles relating to transmission, dispersion, and survival for *Nomuraea rileyi* are also applicable to *Beauveria bassiana*.

BACTERIAL PATHOGENS

Bacterial infections in natural populations of cotton pests are not well documented. Isolations of numerous non-pathogenic bacteria from boll weevils and armyworms (McLaughlin, 1962; McLaughlin *et al.*, 1966) and of *Bacillus cereus* Frankland and Frankland from cotton leafworms (Agudelo and Falcon, 1977) in Colombia have been reported. Bacteria such as *Serratia marcescens* Bizio and others are frequently problems in laboratory rearing of insects but are not considered to be important pathogens in field populations (Bucher, 1963). A possible exception is the report by McLaughlin and Keller (1964). They reported weevil larvae shipped from Mexico being heavily infected by this organism. While pathogenic bacteria probably contribute to low levels of disease in many cotton insect pest populations, they are generally unnoticed in routine scouting of fields.

Bacillus thuringiensis, the entomopathogenic bacterium used in commerce under various trade names, is present in most soils, but again, is not known to cause any appreciable natural mortality in populations of insect pests on cotton. This bacterium

is of potential value as a microbial insecticide and is discussed from that standpoint in Chapter 15.

Bacterial infections have very typical symptoms in lepidopterous larvae. Infection requires that the bacterial cells reach the hemocoel of the insect, either by penetrating the gut wall or through wounds. Once in the hemolymph, bacteria grow rapidly by cell division, utilizing the hemolymph as a particularly rich growth medium. The time sequence of progress of infection may vary with bacterium, host, inoculum level, temperature and other factors, but the infected insect will generally show reduced activity within two to three days. Death of the insect occurs soon after reduced activity is evident. Just prior to death, general body color may begin to darken. After death, cadavers become dark brown to black in color. The integument of caterpillars often remains relatively tough and leathery, resisting rupture when handled. Sucking insects usually darken and retain their body shape, but body contents are initially watery. Microscopic examination of tissue smears of these insects will usually reveal heavy concentrations of bacterial cells.

Diagnosis of bacterial infections is often difficult. Insects dying from physical wounding by predators, physiological causes and pesticide poisoning often show typical bacterial symptoms. Further, they may contain large numbers of saprophytic bacteria which have grown opportunistically in the dead cadavers. Diagnosis of bacteria as cause of death requires demonstration of pathogenicity using Koch's postulates, a time consuming and expensive process. Determination of the species of bacteria associated with a cadaver may reveal those that are known pathogens, but specific isolates of such species may or may not exhibit the characteristic of pathogenicity. Thus, one must be extremely careful in diagnosing bacteria as the cause of death in dead, field-collected larvae.

PROTOZOAN PATHOGENS

Protozoa are single celled animals which have a wide variety of ecological roles, ranging from primary producers to consumers. A large number of species are also parasitic or pathogenic in insects and are, in fact, quite widespread throughout the Class Insecta. Major protozoan groups which contain insect pathogens include the amoeba, ciliates, flagellates, sporozoa and microspora. All members of the latter two groups are obligate pathogens and are highly adapted to this mode of existence. While a considerable volume of literature is available on protozoan infections in species of insects that attack cotton, most of the literature again has dealt with these pest species as they affect other crops, particularly soybean and corn. With the exception of the boll weevil, almost no information is available on the interrelationships between protozoa, pest insects and cotton. One reason for this paucity of information undoubtedly is related to protozoan mode of action and the direct nature of damage that many pests cause in cotton. Many protozoan infections are not lethal, but cause debilitating effects (Brooks, 1988) which may include reductions in feeding, movement and fecundity. Such characteristics would reduce, but not prevent, damage to cotton by bollworms,

tobacco budworms, armyworms, weevils and other insect hosts that feed directly on the flowers and fruits. Thus, heavily infected populations might show reduced damage within generations, but that level of damage could be economically important. The same insect species attacking corn or soybean at similar population levels may be satisfactorily regulated because their economic thresholds are higher.

Only three groups of protozoa will be discussed: the Subphylum Mastigophora; the Class Sporozoea; and the Class Microsporea. The Mastigophora are the flagellated protozoa, and only a small portion of the members of the phylum are insect parasites. All members of the latter two subphyla are parasitic (Brooks, 1988), and both contain members that are obligate insect pathogens. Both the Sporozoa (Class Sporozoea) and Cnidospora (Class Microsporea) characteristically produce spores which provide a mechanism for survival outside of the host insect and which provide mechanisms for infection when ingested by their hosts. One major difference between the two subphyla is the presence of one or more polar filaments in the cnidosporan spore and the absence of this structure in sporozoan spores (Brooks, 1974). These are important features in the infection process, as will be discussed.

FLAGELLATE INFECTIONS

Members of the subphylum Mastigophora characteristically move by means of a flagellum or flagella. Normally, flagellates do not cause high mortality in their hosts, but can cause symptoms that include diarrhea and vomiting. They are typically found within the lumen of the alimentary tract or in organs emptying into it. Flagelletosis is frequently seen in hemipterans, including the green stink bug and certain of the staining bugs of the family Pyrrochoridae. The species *Leptomonas serpens* Gibbs was described from the southern green stinkbug, and *Leptomonas pyrrhocoris* Zotta was originally isolated from a stainer bug, *Pyrrhocoris apterus* (L.) in France (Lipa, 1963). In neither case was the work done on these insects as pests of cotton, but the southern green stinkbug can be a serious cotton pest and related stainer bugs, such as *Dysdercus suturellus* (Herrich-Schaffer) (the cotton stainer), are very likely candidate hosts for *Leptomonas pyrrhocoris* or related flagellates.

Transmission of organisms occurs through eating infective stages of the protozoa which have been excreted or regurgitated onto or into host substrates. *Leptomonas serpens* is known to be passed in this way to plant sap where it can grow and be picked up later by subsequently feeding insects (Gibbs, 1957). The organisms normally attach to the gut or other organ walls and grow and reproduce to large numbers at these sites. Diarrhea is the principal symptom in these cases. In some hosts, the flagellate is able to enter the hemocoel and cause more serious damage, evidenced in *Pyrrhocoris apterus* as lowered activity, lighter color and thicker, whitish hemolymph (Lipa, 1963).

SPOROZOAN INFECTIONS

McLaughlin (1965 a,b; 1967,1971) conducted extensive work on the relationship between the sporozoan *Mattesia grandis* McLaughlin and the boll weevil. This pathogen infects larvae following ingestion of spores. These release numerous smaller

infectious sporozoites which are able to pass through the intestinal wall and reach the fat body inside the body cavity. There, they multiply rapidly through several developmental stages until they ultimately form more spores (Figure 23). Mortality may begin as early as seven days but McLaughlin found peak mortality to occur at 14 days post-inoculation. Adults were also susceptible, and infection reduced both egg production and adult longevity in laboratory studies (McLaughlin, 1965b).

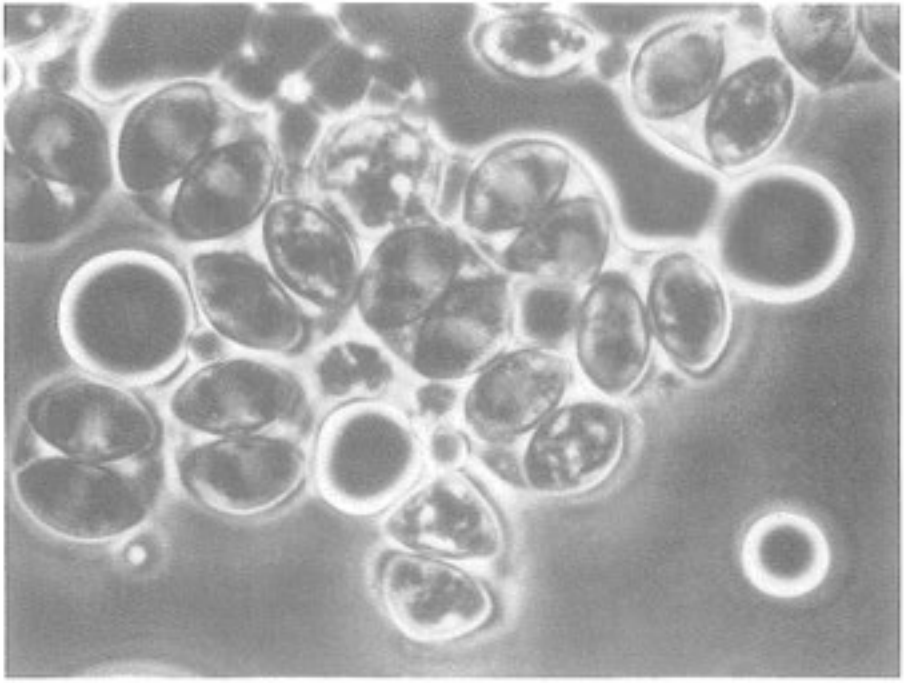

Figure 23. Gametocytes of the sporozoan *Mattesia grandis*, each containing two oocysts, from boll weevil fat tissue. (Phase contrast microscopy) (Courtesy of R. McGaughlin.)

This pathogen was found originally in laboratory cultures of weevils in Mississippi, but McLaughlin (1965a) speculated that it may have entered the colonies from material that was field collected in Tamaulipas, Mexico. He and his colleagues conducted extensive field tests with this pathogen (see Chapter 15).

CNIDOSPORAN INFECTIONS

A second protozoan group, the microsporidia, are found in a large number of insect species that attack cotton, but little work has been done on them as they influence this crop. The pathogens are members of the genus *Nosema* and are found in most lepidopterous pests of cotton, the green stinkbug (Personal communication, J. Maddox,

Illinois National History Survey, Champaign, Illinois), the boll weevil (McLaughlin, 1969) and probably many others. These pathogens, depending on dosage and on the specific host-pathogen involved, may be lethal or debilitating in their action on their hosts.

The microsporidia, like the sporozoans, have a complex life cycle composed of many successive and morphologically distinct stages (Brooks, 1974). The extrahost stage is a somewhat resistant spore (Figure 24) which can exist outside of the host for some

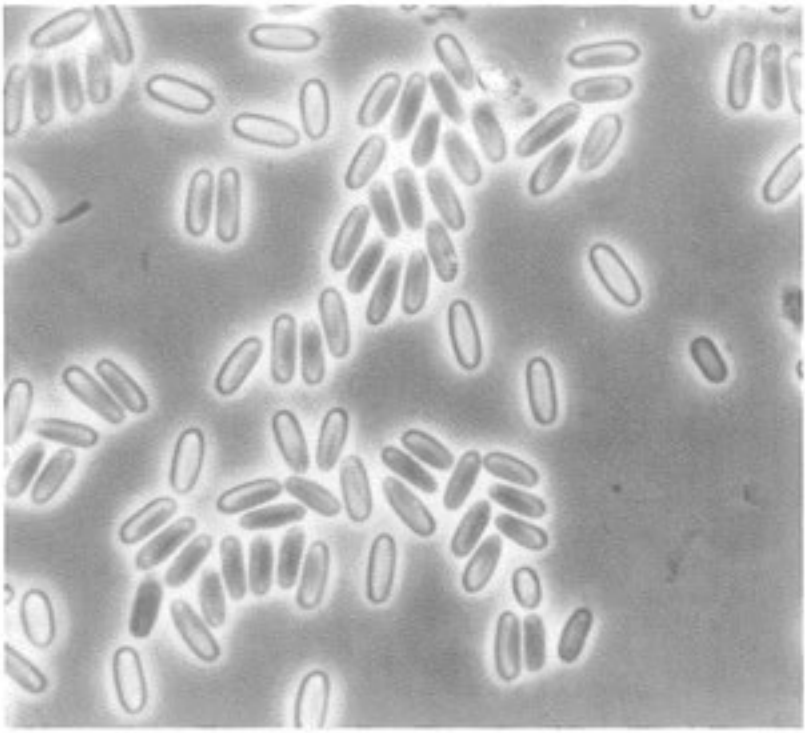

Figure 24. Mature spores of a microsporidian typical of those seen in the hemolymph of infected larvae. (Phase contrast microscopy, 2000X). (Courtesy of W. M. Brooks.)

period of time. It must be ingested to initiate an infection. The spore contains a long hollow tube, the polar filament, which lies tightly coiled within the spore (Figure 25). This filament is forcefully released from the spore once inside the insect's gut. It serves as a sort of living hypodermic needle to aid in infecting the host. A small piece of tissue, the nucleated sporoplasm, is ejected through this tube. If the polar filament is oriented in the gut in such a way that its eversion, or forceable release, results in penetration of the gut wall, the sporoplasm will be placed inside the hemocoel or fat body and will begin developing. Inside the cytoplasm of susceptible tissues, the pathogen multiplies through a series of stages involving nuclear divisions, nuclear and cytoplasmic division, formation of several morphologically distinct stages and ultimately spore formation.

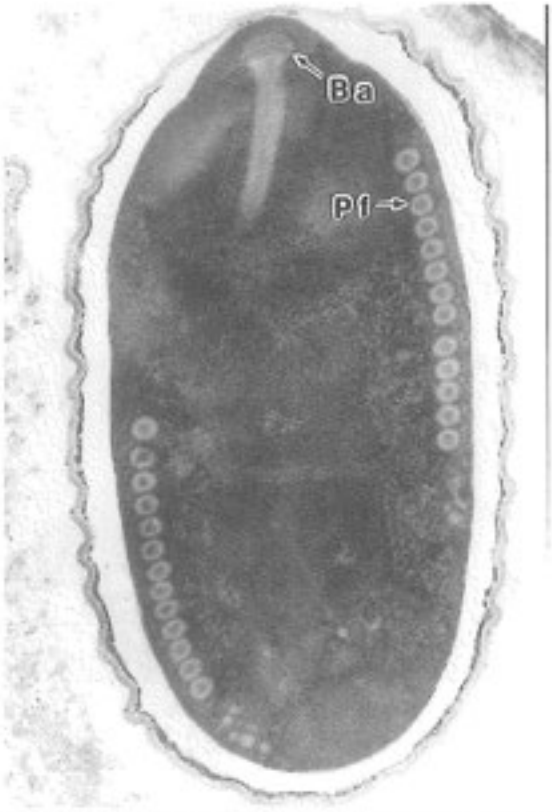

Figure 25. Thin section of a microsporidian clearly showing the coiled polar filament (Pf) and its basal attachment point (Ba). (TEM, 20,000X.) (Courtesy of C. B. Moore.)

Tissues infected vary with host and microsporidian species involved, but most frequently infection involves the fat body (Figure 26) with subsequent infection of silk glands, epidermis, gut epithelium, Malpighian tubules, nerve tissue and hemocytes (Brooks, 1974). The infectious process, from spore ingestion to spore production may require from few to many days, depending on temperature, dosage, and other factors.

Infection by microsporidia may be either chronic or acute, depending on the host, pathogen, dosage, environment and other factors. Frequently, mortality does not result from infection, but feeding and reproductive capacity are reduced. Thus, infected populations tend to cause much less damage than would be caused by equal numbers of healthy individuals.

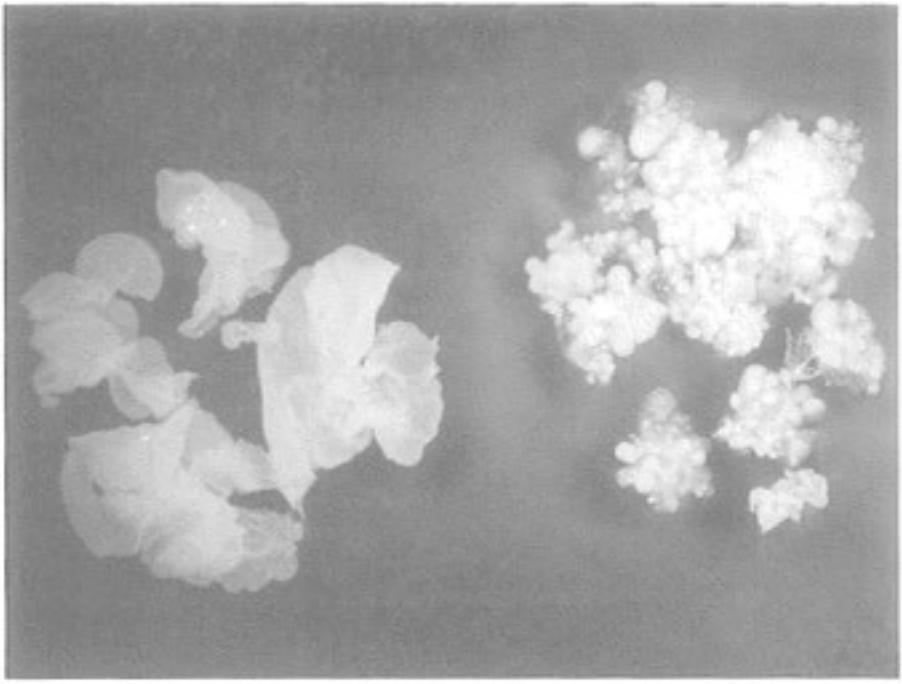

Figure 26. Comparison of fat body tissue from healthy (left) and *Vairimorpha*-infected (right) bollworm larvae. Note milky cloud around infected tissue caused by released spores. (About 5X.) (Courtesy of W. M. Brooks.)

Cotton pests known to suffer from microsporidiosis and the pathogens involved include: *Heliothis* and *Helicoverpa* spp. by *Nosema heliothidis* Kramer (Figure 27) and *Vairimorpha necatrix* (Kramer) (Figure 24); the southern green stinkbug by an undescribed microsporidian (Unpublished data, J. Maddox, Illinois National History Survey, Champaign, Illinois), the boll weevil by *Nosema gasti* (McLaughlin) (McLaughlin, 1969); and the cabbage looper by *Nosema trichoplusia* Tanabe and Tamashiro (Tanabe and Tamashiro, 1967). This list is not exhaustive or complete. A complete list would be complicated by the question of cross-infectivity (Brooks, 1988) since all of the above pathogens have been shown to be highly cross-infectious to other species. For example, *Nosema gasti* was infectious to many Lepidoptera including the important cotton pests—the tobacco budworm, pink bollworm, bollworm and cabbage looper (Ignoffo and Garcia, 1965).

While little work has been done on these pathogens in relation to cotton, they are very likely present and possibly at times prevalent in field populations. If cotton production should become less dependent on chemical pesticide inputs in the future, these pathogens will likely receive much more attention.

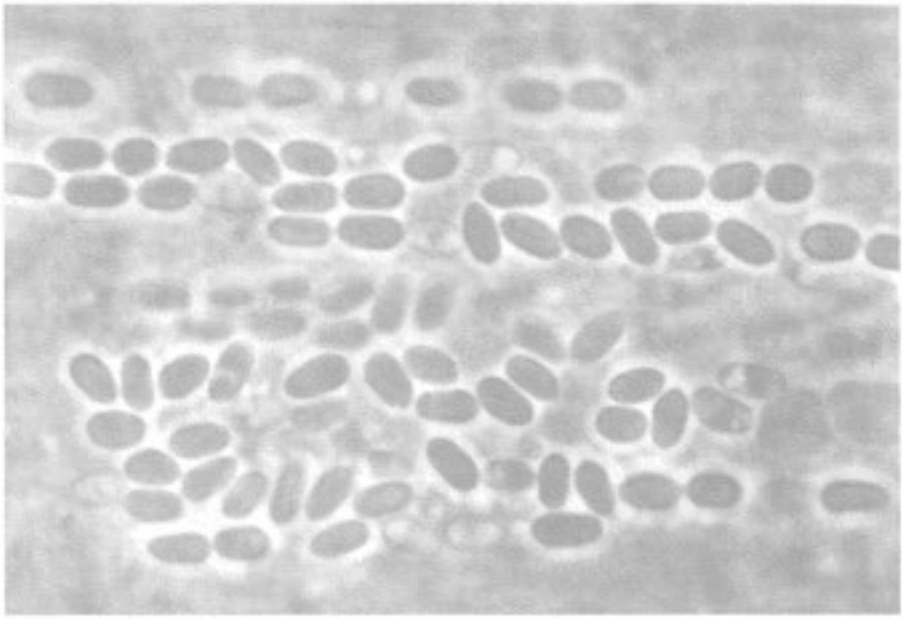

Figure 27. Spores of *Nosema heliothidis* in midgut tissue of bollworm (wet mount, phase contrast microscopy, about 1800X). (Courtesy of W. M. Brooks.)

NEMATODES

A wide variety of nematodes have been reported as obligate or facultative endoparasites of many insect species. Parasitism by nematodes may result in sterility, reduced fecundity, delayed development, aberrant behavior or host death. These effects may play a significant role in regulating insect populations (Kaya, 1987). Although numerous reports of nematode parasitism in insect populations have been published, only a few of these are from insects found in cotton. Those reported from cotton insects fall into three families: Mermithidae; Steinernematidae; and Heterorhabditidae. Members of the Mermithidae can easily be distinguished from the other two families by the size and numbers of nematodes found in each insect host. If a host contains only one or two worms that measure one inch or longer, the nematode is probably a mermithid. Hosts parasitized by steinernematids and heterorhabditids will usually contain several thousand or more juvenile nematodes (0.2 to 0.5 millimeter) and some larger adult nematodes (1 to 5 millimeter) (Nickle, 1974).

MERMITHIDS

The mermithids constitute a large group of obligate parasites of invertebrates. They are common in both terrestrial and aquatic environments and are generally host spe-

cific for a small group of insects. Mermithids are nearly always lethal to their host and most are considered to have potential as biological control agents (Peterson, 1982).

Mermithids are relatively long nematodes, with some adults reaching a length of 11 inches (30 centimeters) in insect hosts. They are usually light colored, appearing as whitish worms when observed emerging from their hosts. Most mermithids have a direct type of life cycle. The short-lived, non- feeding infective-stage juvenile emerges from an egg and searches for a host. Using its stylet, it bores through the insect's body wall and enters the hemocoel where it develops. After a development period of five days to several months, depending on the species, the full-grown parasite emerges, molts to the adult stage in the environment, mates and deposits eggs (Poinar, 1983).

Although there are hundreds of reports of mermithid parasitism, very few are from cotton insects and most of these are from host plants other than cotton. Stadlebacher *et al.* (1978) reported parasitism levels of 39 to 47 percent by *Hexamermis* spp. in bollworm larvae collected from clover and vetch in Mississippi. Nickle (1978) reported parasitism of the fall armyworm by *Hexamermis* spp. in Nicaragua. This same nematode infected the beet armyworm, under laboratory conditions. Puttler *et al.* (1973) reported a 64 percent level of parasitism by *Hexamermis arvalis* in the black cutworm, *Agrotis ipsilon* (Hufnagel), from corn.

STEINERNEMATIDAE AND HETERORHABDITIDAE

Members of these two families are entomogenous nematodes which have been recovered from many areas throughout the world. They are selective for insects and a few other arthropods, but do not adversely affect mammals or plants. Because they kill their hosts rapidly (24 to 48 hours) and have a wide host range there has been a great deal of interest in their use as biological control agents (Woodring and Kaya, 1988). Because of similarities in their life cycles, the two families will be discussed together.

Like most members of the order Rhabditida, the steinernematids and the heterorhabditids are bacterial feeders, but they differ from other rhabditids by having a mutualistic association with specific bacteria in the genus *Xenorhabdus*. Two species of these bacteria are recognized. *Xenorhabdus nematophilus* (Poinar and Thomas) is a non-pigmented associate of steinernematids, and *Xenorhabdus luminescens* Poinar and Thomas is a red-pigmented, bioluminescent symbiont of heterorhabditids. These bacteria do not have an environmentally resistant stage and have never been isolated except from their nematode vectors or their vectors' insect hosts (Woodridge and Kaya, 1988).

Like most nematodes, members of these two families have a simple life cycle that includes the egg, four juvenile stages and the adult. The infective stage is a special third stage juvenile or dauer larva which is ensheathed within a separate, but still intact, cuticle from the previous juvenile stage (Figure 28) and is particularly resistant to environmental conditions. These infective juveniles contain live cells of the mutualistic bacterium in their intestines and function as vectors of the bacterium. The infective nematodes locate a host and enter through natural body openings—mouth, anus or spiracles. They then penetrate through the midgut wall or tracheae into the hemo-

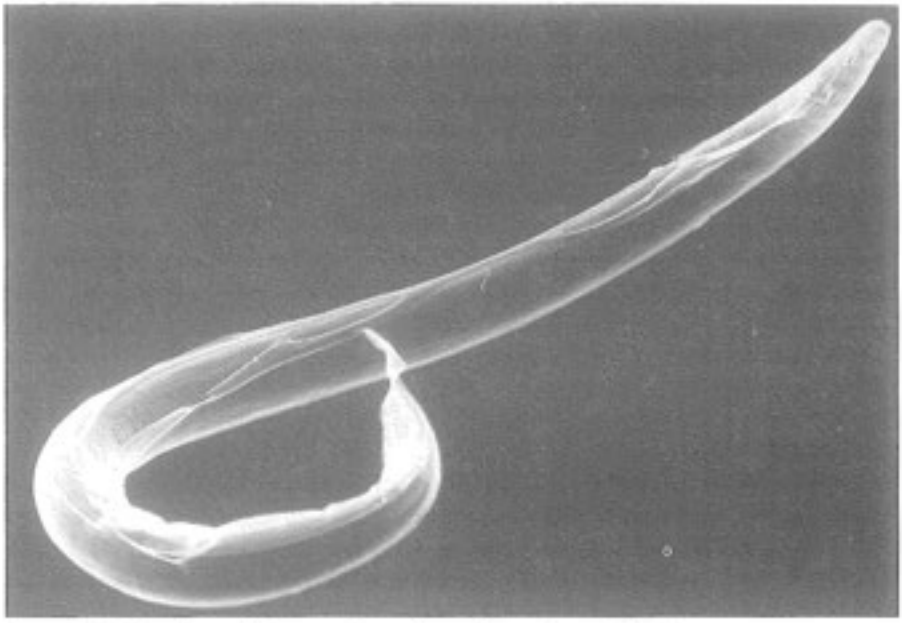

Figure 28. Infectious third stage juvenile or dauer larva of *Steinernema carpocapsae* (Family Steinernematidae). Note the wrinkled outer sheath evident near the lower posterior end of the body. (SEM, 560X.)

coel. The infective juveniles of the heterorhabditids differ from the steinernematids by having a tooth. They are able not only to enter through natural openings, but also may directly penetrate through soft areas of the cuticle of a host. Once in the hemocoel, the nematodes release the bacterium which rapidly multiplies and kills the host within 48 hours. The immature nematodes feed on the bacteria and develop to adults which mate and produce progeny. The nematodes will pass through two or three generations within the host. When conditions are suitable, the infective juveniles will exit the cadaver to seek new hosts. The entire cycle requires 10 to 14 days (Woodridge and Kaya, 1988).

Although members of these two families are known to be widespread and are commonly isolated from soils, there are very few reports of their natural occurrence in cotton insects. Poinar (1975), in his original description of the family Heterorhabditidae, reported that the original collection of the type species, *Heterorhabditis bacteriophora* Poinar, was from a pupa of *Helicoverpa punctigera* from Australia. Kahn *et al.* (1976) described another species of nematode in the same genus, *Heterorhabditis heliothidis* Kahn, Brooks, and Hirschmann from prepupal and pupal specimens of the bollworm from North Carolina. Poinar (1990) now considers both of these to be the same species, *Heterorhabditis bacteriophora*. Recently, Cabanillas *et al.* (1994) described a new species of steinernematid nematode, *Steinernema riobravis*, which was originally found infecting bollworm and fall armyworm in corn fields in the Lower Rio Grande

Valley near Weslaco, TX (Raulston et al., 1992). This species is of interest because it appears to be adapted to a semi-arid environment and can survive at higher soil temperatures than can other species in this genus (Cabanillas *et al.* 1994). No reports have been made on its natural occurrence in cotton, but it may have promise for development as a control agent for these and other cotton pests because of its adaptation to hot, semi-arid environments. Akhurst and Brooks (1984) conducted a survey for steinernematid and heterorhabditid nematodes in North Carolina. They collected over 500 soil samples from cropland, pasture, and forest habitats at 53 sites. Nematodes were isolated from 25 of the sites and were more common in cropland and pastures than in forest soils. Heterorhabditids were more abundant (84 percent of isolates) than steinernematids. It is probable that nematodes of both families are present in cotton fields and cause mortality in those insects which spend part of their life cycle in the soil.

SUMMARY

It is evident from the information presented in this chapter that the large number of pest insects and mites associated with cotton has an even larger number of microbial and nematode pathogens associated with them. Most of these do not occur predictably at sufficiently high incidence levels to produce noticeable natural reductions of their host populations. Notable exceptions do occur, such as the epizootics of nuclear polyhedrosis virus in cabbage looper populations and of the fungus *Neozygites fresenii* in cotton aphid populations. Some, such as the NPV of the beet armyworm or the fungus *Neozygites floridana* on twospotted spider mites may occur in high incidence in some fields in some years, but not consistently. Most, however, occur either in such low levels that they are rarely noticed, or they are overlooked because their symptoms do not allow for ready diagnosis or recognition.

Individually and collectively these pathogens are very important in cotton pest management, and have far greater potential than has been realized to this date. As natural mortality factors, some contribute significantly to suppression of their host populations. Others, as has been pointed out throughout this chapter, are currently of value or have potential future value for development as microbial control agents. As the boll weevil eradication program expands across the cotton belt of the United States, less pesticide use on cotton will result in opportunities for managing other pests in different ways than at present. Reliance on naturally occurring or artificially manipulated pathogens has considerable promise for current and future insect and mite management programs.

There is a definite information gap on pathogen-host relationships in cotton. As stated previously, most information on pathogens from cotton pests has been collected from other crop systems. Until this knowledge gap is filled, we will be unable to fully appreciate and take advantage of the roles that these organisms are playing or can play in cotton insect and mite pest management.

SECTION II

TECHNOLOGICAL COMPONENTS OF INSECT AND MITE MANAGEMENT

Chapter 6

MODELING AND COMPUTERIZED DECISION AIDS

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INTRODUCTION

Entomologists have long recognized the challenge to acquire relevant information and effectively use it for problem solving; however, the complexities of entomological problems have frustrated these efforts. Insect problems in agriculture rarely are due to the occurrence of single species, a fact that is particularly true in cotton. Instead, they involve communities of plants and animals. Understanding multiple species and their interactions are difficult undertakings, partly because the methods of study have not been well defined. The same difficulty holds true in applying useful information to problem solving. Notwithstanding, events of the last forty years have provided new opportunities to gather and apply information.

During the period between 1920 and 1930, the boll weevil, *Anthonomus grandis grandis* Boheman, greatly curtailed cotton production in the Southeast, forcing it to the weevil-free areas of the West (Frisbie *et al.*, 1989). The situation changed after World War II, and the rapid development of agricultural chemicals and on-farm mechanization dramatically altered cotton production and pest management throughout the Cotton Belt. Initially, chemicals were relatively cheap and, as they increased in number and efficacy, farm production and profits rose. Mechanization, improved varieties and high inputs of pesticides, fertilizers and water brought on a "green revolution" in all of agriculture. At the same time, these changes institutionalized a near single-tactic approach to pest management. Inevitably, the heavy dependence on chemicals changed the way of doing business in crop production, agricultural research, extension and the chemical industry. Alternative management approaches, and the acceptance of some pest losses common before the war, were forgotten in a new generation.

The benefits of a single-tactic management system were soon being weighed against developing problems. These problems intensified over the years and included the destruction of nontargeted species (including beneficial arthropods, fish, birds and mammals) and the buildup of secondary pest populations. Pesticide resistance resulted in control failures, greater chemical usage, and increasing costs of control. Environmental contamination, such as that found in groundwater, ultimately led to public health concerns and pesticide registration cancellations. These serious consequences sparked a strong and lasting debate within the political, scientific, agricultural and lay communities that challenged farm management practices and its heavy reliance on chemicals. Increasingly, the unilateral approach to pest management came under attack because of the associated social, economic and environmental costs involved. To those who made their living from agriculture, the unsettling question arose—what to do next?

Managers of food and fiber resources often deal with insect pests in one of two ways: through direct control at times of crisis (e.g., during insect outbreaks) or through direct control when no control is needed (e.g., when insect populations are below thresholds or at endemic levels). In the first case, managers are willing to accept the risk of insect attack, a situation sometimes found in forestry because of the relatively low crop value. In the second case, managers are unwilling or unable to accept risk. They usually deal with crops of high value such as those found in production agriculture. Cotton is an excellent example.

Unfortunately, both management strategies are inappropriate, and economics are only partly to blame. Management problems often result from a lack of knowledge or an inability to access and effectively use existing knowledge. Thus, having information available in a general sense and not being able to access or use it effectively is a dilemma which affects all levels of crop production. This dilemma has hindered the application of integrated pest management (IPM) as it was originally conceived. Unlike single-tactic approaches, IPM requires a great deal of integrated information on the dynamic status of crops, insects, pest impact, control tactics and cost/benefits to determine the appropriate management alternatives. The inability to integrate, interpret and transmit meaningful information quickly to those who can use it has had no adequate solution until recently.

Just as synthetic chemicals transformed agro-management after World War II, another transformation in crop and pest management began in the late 1960s. By this time the political and social climate favored a major increase in research funding directed toward developing new approaches to agroecosystem management. In 1972, the National Science Foundation, Environmental Protection Agency (EPA), and the United States Department of Agriculture (USDA) sponsored a massive commitment to integrated pest management on six major cropping systems in the United States: alfalfa, apple, citrus, cotton, soybeans, and pine forests. Cotton was studied under the "Huffaker Project" (1972-1978), along with alfalfa, apple, citrus and soybeans. This project was replaced by the Consortium for Integrated Pest Management (CIPM) project which excluded citrus and was funded by the EPA from 1979-1981 and the USDA,CSRS (Cooperative State Research Service) from 1981-1985 (Frisbie, 1985).

These multidisciplinary research projects involved about 250 scientists from numerous universities, state experiment stations and federal laboratories across the country. Their primary goal was to develop socially and ecologically sound management systems that optimized the costs and benefits of crop production and protection. Such management systems would require a great deal of information on the various important components of the agroecosystem—on the dynamic status of the crop, pests and beneficials; on the environment; and, on the costs and benefits of making alternative management decisions. In addition, the information on the various system components had to be formulated in such a manner as to explain component interactions. Systems science and mathematical modeling were proposed to unify and describe the complex dynamic components and their interactions. Advancements in computer technology made this approach feasible.

SYSTEMS ANALYSIS AND POPULATION MODELING

Computers were emerging as a revolutionary new technology during the 1950s, with applications first in research and later in business. Like the rest of the research community, agricultural scientists quickly identified applications for this powerful tool. One prominent use was in areas of population ecology and modeling, fields heavily dependent on numerical analysis. By the early 1960s, a systems approach was gaining acceptance as the means for understanding, describing and studying crop ecosystems (e.g., see Watt, 1961, 1966; Clark *et al.*, 1967; Getz and Gutierrez, 1982). Watt (1966) defined a biological system as a group of interacting and interdependent components forming a unified whole. Components under study could be the cell, organism, population or community. IPM investigators endorsed the population level of organization because the combined effects of individual pests on a crop could best be explained using this level of complexity.

The processes of describing, explaining and controlling system behavior over time are collectively called systems analysis (Curry and Feldman, 1987). Getz and Gutierrez (1982) defined systems analysis somewhat differently, although appropriately for this discussion, as the application of quantitative and qualitative techniques that enhance the understanding of interactions among components of a crop-pest system and their relationships to the environment and management practices.

MATHEMATICAL FOUNDATIONS OF POPULATION MODELING

Reviews describing the mathematical foundations of population modeling in natural and agroecosystems are provided by Getz and Gutierrez (1982) and Curry and Feldman (1987). Early investigators interested in modeling interactive populations proposed a system of differential equations (Lotka, 1925; Volterra, 1926; Nicholson and Bailey, 1935). These models were not adequate to describe system components and their interactions because they ignored the age structure of populations and considered all individuals to be equal. Leslie (1945) developed a convenient mathematical form to describe the various age classes of a population using matrix algebra, but this discrete time approach modeled the mean value of population growth; e.g., indi-

viduals of a cohort (those born at the same time) have identical rates of development. Using a system of partial differential equations, von Foerster (1959) proposed a continuous time model with age-dependent population growth.

Gutierrez *et al.* (1980, 1985) provided a historical review of specific modeling efforts in cotton. Early work concentrated on understanding plant physiology, especially as it relates to respiration and photosynthesis. This work led to the development of the cotton model, SIMCOT II — primarily a USDA, Agricultural Research Service (ARS) effort that provided mechanistic detail of the growth and development of a single (average) plant (Baker *et al.*, 1972; Jones *et al.*, 1974; McKinion *et al.*, 1974). This model predicted discrete numbers of squares and bolls (fruit) produced by a plant. Fruit production of a population of plants was estimated simply as the number of fruit per plant times the number of plants in the population. Because insects normally show oviposition and feeding preference to fruit of certain age classes, IPM investigators required that the number of fruit per area vary continuously among plants in the population. SIMCOT II ignored the continuous age structure in the cotton crop and thus was not endorsed, although some of the physiological parameters were used in the ensuing IPM models. For this reason, and because of the high degree of interaction among IPM research groups, later cotton models were very similar in structure and generally were based on a system of von Foerster-type equations.

These crop models basically described a population of plants of different ages, each plant comprised of sub-populations of roots, stems, leaves and fruit of differing ages. Cohorts of leaves produce photosynthate at age-dependent rates which is allocated to respiration, reproduction, vegetative growth and reserves. Mortality of plant organs occurs as a function of age and extrinsic factors, such as insect herbivores (plant-feeding insects). The underlying patterns of plant growth and development are determined by weather, nutrition and water. Arthropod pests affect the plant by attacking the carbohydrate supply side (e.g., defoliators and most diseases), the demand side (e.g., squares or bolls) or both sides of the photosynthetic production/allocation process.

Three major cotton/insect modeling groups were established during the IPM projects of the 1970s and 1980s. These interdisciplinary research teams were located at the University of California, Mississippi State University, and Texas A&M University. Some were made up of both state and federal (ARS) personnel. Each developed its own cotton model, which are remarkably similar in general structure. They concentrated on particular pest species, developing population models that were integrated with the cotton models. Another group at North Carolina State University also made early contributions to the insect modeling effort. An independent ARS effort developed SIMCOT II and later GOSSYM, but this effort was not involved with insect modeling until recently.

COTTON INSECT MODELS

This section summarizes the prominent population models that describe cotton insect pests found in the United States. It also lists some process-level models not

incorporated in the population models. Model descriptions are not complete in listing or detail. No attempt is made to evaluate model performance (the degree to which they represent the "real world"). The section is organized alphabetically by insect name, followed chronologically by model citation.

BEET ARMYWORM, *Spodoptera exigua* (Hübner)

The beet armyworm was introduced into North America during the nineteenth century and presently is found throughout the western and southern regions of the United States (Hogg and Gutierrez, 1980). The species feeds on multiple hosts (polyphagous) and has multiple generations each year (multivoltine). It overwinters as adults and is only able to survive in areas where the winters are mild (apparently it does not diapause). The excellent migratory ability of the insect permits expansion into favorable areas. Females oviposit eggs in clusters that are covered with scales. Young larvae feed gregariously near the egg cluster and gradually disperse as they grow. Pupation occurs in the soil.

The insect is a secondary pest of cotton. Besides being a defoliator, it attacks plant terminals and squares. There is one population model of beet armyworm, developed by Hogg and Gutierrez (1980) at the University of California.

Hogg and Gutierrez (1980) — This model stresses beet armyworm flight phenology (the timing and patterns of flight activity) under California conditions. It contains descriptions of births and deaths through time and thus can be classified as a population model. Important processes described in the model include immature development and mortality, oviposition, adult longevity and female flight activity. The model uses a Leslie matrix structure.

Oviposition of the beet armyworm does not commence until the third day of adult life. An exponential function is used to describe the cumulative percent oviposition relative to adult age (measured in degree days above 50F [10C]). Total fecundity varies with temperature, female size and the host on which the insect was reared; however, for modeling purposes an average value of 900 eggs per female is used.

A linear, degree-day (DD) model is used to describe the relationship between development rates and temperature. The model is parameterized with data from constant temperature experiments, with larvae reared on artificial diet. Development times of larvae and pupae are combined because the precise timing of pupation could not be determined once larvae entered the soil (to pupate). The lower threshold of development is estimated by regression methods at 54F (12.2C).

Age-dependent survivorship of eggs and larvae is modeled with an exponential function, using a constant age-specific mortality rate. Survivorship of adult females is both age- and temperature-dependent.

Hogg and Gutierrez (1980) studied the possible effects of three variables (wind, moonlight and night temperature) on female flight activity. High winds dampened moth catches in traps, but it occurs infrequently during the summer and thus was not included in the model. Moonlight was not correlated with trap catch. The influence of night temperatures (in degree-days) on trap captures (percent of maximum catch) is

described by an exponential equation. The lower and upper threshold values for flight are set at 60.1F (15.6C) and 90F (32.2C), respectively.

The model is initialized with light trap data in the early season and predicts the subsequent pattern of moth captures through time. Predictions compared favorably to light trap catches for the San Joaquin and Sacramento Valleys. The model performed poorly for the cooler Salinas Valley. The investigators noted that differences in model performance by location are due to a lack of understanding and description of one or more of the variables influencing flight, population growth or development.

Process Models Not Associated With The Population Model — Gutierrez *et al.* (1975) modeled the combined effects of defoliation by beet armyworm and the cabbage looper, *Trichoplusia ni* (Hübner), on cotton growth and yield. Like beet armyworm, the cabbage looper is a secondary noctuid pest of cotton that may reach outbreak proportions following pesticide use. In this model, females show ovipositional preference to leaves of an intermediate age class (between 840 and 1500 degree-days Fahrenheit). Larvae attack and consume these leaves first, and when they are all consumed, larvae move to both younger and older leaves. Larvae consume leaves at an age- and time-dependent rate. The amount of leaf dry matter required by the larval population is a product of the number of larvae in different age cohorts and the daily rate of consumption by larvae in each cohort. The rate of consumption varies exponentially with larval age. The number of larvae in the population is based on field counts, and this value is used as a model input. The computer results indicated that moderate defoliation causes only slight yield reductions. The investigators concluded that either the model is incorrect, grossly insensitive, or that larval feeding has a physiological effect not accounted for in the model.

BOLL WEEVIL, *Anthonomus grandis grandis* Boheman

The boll weevil is native to Central America where it is host specific to plants of the tribe Gossypieae of the family Malvaceae, which includes several species of cotton. This insect forms a unique relationship with its host (Gutierrez *et al.*, 1979a). In the United States, it is an obligate monophagous species (feeding restricted to one kind of plant) dependent on commercial cotton for its survival. Recently, the eradication program has eliminated the boll weevil as a pest from Virginia, the Carolinas, Georgia, Florida, Arizona and California.

The boll weevil has a multivoltine (completes more than one generation each year) life-cycle. Newly emerged adults prefer feeding on pollen of open flowers. After a day or so, its elongated rostrum enables the adult to penetrate the flower bud (square) and feed on immature anthers before bud opening. Females search cotton plants, showing ovipositional (egg laying) preference to flower buds measuring about 0.118 to 0.354 inches (3 to 9 millimeter) diameter (Lincoln *et al.*, 1963). Pristine squares normally are selected for oviposition, but when they are scarce, oviposition may occur in squares containing an egg or in cotton bolls (Walker *et al.*, 1977; McKibben *et al.*, 1982; McGovern *et al.*, 1987). The insect has three larval instars that feed cryptically

(unseen) in squares or bolls. In response to a developing weevil (second and third instars), fruit generally are shed from the plant after about five to nine days (Coakley *et al.*, 1969; King and Lane, 1969). The loss of fruit from the plant results in significant changes in the microhabitat of the developing weevils. This can lead to high mortality. The weevil has few natural enemies; however, the parasite *Bracon mellitor* Say attacks third instar larvae and can cause from 5 to 50 percent mortality to first generation larvae (Bottrell, 1976). Fire ants also suppress weevil populations in certain areas (Sterling, 1978).

Currently there are five population models of the boll weevil. They were developed by the USDA,ARS in Arizona (Fye and Bonham, 1972), North Carolina State University (Jones *et al.*, 1977), the University of California (Wang *et al.*, 1977 and Gutierrez *et al.*, 1991a) and Texas A&M University (Curry *et al.*, 1980).

Fye and Bonham (1972) — Using insectary data on adult longevity and fecundity (egg-laying capacity) (Fye, 1969), Fye and Bonham (1972) described the cumulative percent oviposition of females emerging from overwintering sites and those of later generations as functions of adult age. Daily oviposition of the population is mathematically described using these estimates, together with the mean lifetime fecundity per female and the number of females emerging each day.

A linear regression model is used with a rate summation approach to determine development times as a function of temperature. Model coefficients are obtained from data on colony weevils reared on artificial diet from eggs to adult emergence (Fye *et al.*, 1969). Input temperatures driving the model vary according to the location of the infested squares. For example, several equations describe the temperature in squares on the plant or in squares on the ground as functions of air temperature (for upland or extra long-staple cotton). The proportion of infested squares aborting through time is determined from a cumulative function. Separate temperature equations are used for weevils in bolls because these weevils normally cannot emerge until the boll matures and opens (a unique feature of Arizona weevil populations). For this reason, a temperature-dependent boll maturation routine is provided.

Fye and Bonham (1972) described temperature-dependent mortality of immature weevils in squares on the plant (before abscission) and immatures in squares on the ground (after abscission). Noting that 35 percent of the punctured squares on plants fail to abort, they postulated that eggs are killed by temperatures above 100F (37.8C). For weevils in squares on the ground, percent mortality is described as a function of the time spent above 100.4F, the lethal temperature (Fye and Bonham, 1970). Descriptive equations estimate adult longevity of weevils emerging from overwintering sites and those of later generations [data from Fye (1969)]. Estimates of daily mortality are used with daily emergence to calculate the number of weevils in the population.

Jones *et al.* (1977) — This comprehensive behavioral and mechanistic model calculates the number of squares and bolls damaged by adult weevils on a given day. Reproducing females are treated separately from non-reproducing females and males

(Jones *et al.*, 1975a,b). Factors considered in the model are fruit availability; the number, age and sex structure of the weevil population; and the searching, feeding and oviposition behaviors of the weevil.

Feeding and oviposition only occur during daylight hours (Cushman, 1911). Average hourly feeding rates vary with female age and depend on the mean number of eggs oviposited per hour, the amount of food ingested per oviposition event, the total ingestion per hour and the mean ingestion per feeding event. Oviposition depends on the availability of eggs in the oviduct, preferential site selection of fruit and the availability of sites in the field [determined by their cotton model, COTCROP (Jones *et al.*, 1980)]. Individual females make one puncture per fruit and do not discriminate against previously punctured sites (e.g., selection of a site is not affected by the number of punctures already present at the site). After oviposition, females move to another site before feeding or ovipositing again. Weevils may feed without ovipositing, depending on their energy balance. Searching for an oviposition site commences only when a mature egg is available in the oviduct. Egg production rates differ from oviposition rates. The time to complete an oviposition event is constant, but searching time varies with fruit density and searching rate.

Females preferentially select food and oviposition sites in this order: (a) squares older than 10 days, (b) squares 5 to 10 days old and bolls less than 7 days, (c) bolls 7 to 19 days old, and (d) plant terminals and leaves. Initially, females accept only class (a) sites, but if these sites are not encountered after a certain time of searching, other sites of lower ranking are accepted. Searching occurs randomly and assumes that fruit are uniformly distributed in the field. The data used to develop these submodels are derived from numerous sources—Hunter and Pierce (1912), Mitchell (1967), Lloyd *et al.* (1961), Mitchell and Cross (1969), and Mitchell *et al.* (1973).

The submodels do not account for known environmental influences (such as temperature and food type) on any of the processes (such as egg production rates, oviposition, feeding and searching rates). Many parameter values are undefined due to the lack of experimental data. Because the data to parameterize and validate the models are difficult to obtain, the individual process models are largely unvalidated.

Jones *et al.* (1977) used the exponential equation of Moore (1972) to predict the mean development times of eggs, larvae and pupae as a function of temperature. The inverse of predicted time is used to calculate the mean developmental rate because time cannot be accumulated under variable temperatures. The model does not describe decreasing rates above the optimum (the temperature at which development is the fastest), but rather it approaches an asymptote at high temperatures. The investigators may have selected this model because the data on which it is based (Bacheler and Bradley, 1975; Bacheler *et al.*, 1975) do not extend beyond the optimum for most life stages. The lower threshold of development is 57.9F (14.4C) (Hunter and Pierce, 1912). To account for variability in development times among individuals of the same age group, development times vary between $\pm$ 2 standard deviations of the mean. A cumulative normal distribution is then used to predict the probability that an insect completes development (of a given stage) in any time period.

Temperature-dependent mortality of boll weevil larvae and pupae is described using a relationship based on the hours spent above or below an optimum temperature. Model constants are derived using the experimental data of Bacheler *et al.* (1975). Daily predation and parasitism are held constant for each stage and are estimated from the data of Hunter and Pierce (1912). Insecticides kill only adults at a constant rate and only on the day of application. The influence of temperature on adult longevity is treated the same as other life-stage transitions [model coefficients are determined using data of Isely (1932)].

Wang *et al.* (1977) — These investigators emphasized the role of nutrition on weevil reproduction, describing the oviposition period and the rate of egg production as functions of the nutritional history of the female [data from Isely (1928) and Cushman (1911)]. The nutritional status of a weevil depends on the number of squares, small bolls and large bolls available to its parent at the time of oviposition, and the preference the ovipositing female has for these sites. Females are fecund between the ages of 265 and 1000 degree-days (measured in degrees Celsius), but the actual oviposition period varies with nutritional history. For example, the ovipositional period of square-reared females is 1.5 times longer than that of females reared on small bolls. The egg production rate also changes as a function of the insect's nutritional history. Overall, females produce an average of 200 eggs in their lifetime, but square-reared females produce four times as many eggs as females reared on small bolls. Oviposition ceases when only large bolls are available.

A linear, degree-day approach is used to estimate development times under fluctuating temperatures. Data for square-reared weevils (Bacheler *et al.*, 1975) and diet-reared weevils (Roach, 1973) are used to calculate the mean number of degree-days (265) from egg to adult emergence. The lower threshold of development is 53.6F (12C) (Fye *et al.*, 1969). Transition times of individual life stages are not considered, nor are the development times of individuals in the population.

Wang *et al.* (1977) proposed a discrete model to describe weevil mortality. Using data of Cushman (1911) and Sterling and Adkisson (1970), the probability of death is 0.37 (37 immatures expected to die per 100) for all immatures combined, 0.43 (43 adults expected to die per 100) for adults between the ages of 265 and 720 degree-days, and 0.2 between 720 and 1110 degree-days. These probabilities are modified by the insect's nutritional history. For example, adults reared on squares live 1.5 times longer than those reared on bolls (Isely, 1928).

Wang *et al.* (1977) defined the maximum rate of boll weevil immigration per acre as 0.704 (704 boll weevils per 1000 expected to enter an acre of cotton). Immigration (entering a field) occurs only in adults of a specific age. Emigration (leaving a field) varies with the supply/demand ratio of oviposition sites in the field.

Curry *et al.* (1980) — Curry *et al.* (1980) modeled the cotton crop/boll weevil system using a von Foerster (1959) framework modified by a system of partial differential equations which were solved by iterative numerical methods (Feldman and Curry, 1983). A distinguishing characteristic of this model is the incorporation of stochastic

elements of reproduction, development and mortality. The model uses four-day time steps for cohort aggregation. Hourly temperatures are used to drive the individual life-process models (e.g., development, reproduction, emergence).

The percentages of weevils emerging from overwintering sites (Hinds *et al.*, 1909) and weevils colonizing cotton (Walker and Niles, 1971) are described with linear functions of cumulative DD above 43F (6.1C) after March 1. No reproduction occurs in the field until the cotton contains squares that are at least one-third grown. Normally, only one egg is allocated per fruit.

Oviposition is estimated using an age-dependent reproductive profile and temperature-dependent rates. For example, each adult cohort that completes development over a four-day period is given a reproductive profile that is developed using the techniques of Curry *et al.* (1978a) and data of Isely (1932) and Cole (1970). This profile is integrated between the starting and ending development dates of each cohort and yields the fraction of total reproductive potential for each time period. This fraction is multiplied by the temperature-dependent lifetime fecundity associated with the period. Values are summed across all cohorts to yield an egg-laying potential of the population given unlimited oviposition sites.

The number of eggs actually oviposited depends on the number of acceptable fruit per acre and a female's searching coefficient (a model constant). This approach approximates some of the complex behavior described in the model of Jones *et al.* (1975b), which was not used because the influences of environmental variables on relevant processes were not defined (Cate *et al.*, 1979) and some of the basic parameters were not measured (Curry *et al.*, 1980). Ovipositing females show preference for fruit of different sizes. Given stable preference probabilities for each size class, the availability of fruit in the field (determined by their cotton model) determines the resulting distribution of deposited eggs. Size classes are declared as: (a) small squares less than 0.276 inches (7 mm) in diameter, (b) one-third grown and large squares greater than 0.276 inches, (c) small bolls less than 0.945 inches (24 mm), and (d) large bolls greater than 0.945 inches. Relative preferences for these size classes are 0.354, 0.85, 0.469 and 0.534, respectively. This work is based on the model of Cate *et al.* (1979), which was validated using several sets of field data including that of Jones *et al.* (1975b).

Curry *et al.* (1980) predicted development times of weevil cohorts using the approaches of Sharpe and DeMichele (1977) and Sharpe and Hu (1980) to describe development rates as a function of temperature and nutrition (e.g., squares *vs* bolls), and Sharpe *et al.* (1977) to describe the variation in development times among individuals in the population. The nutritional component of the model describes the differences in nitrogen content between squares and bolls. This difference affects both mean development times and the variation in development times among individuals feeding on the two food sources. The approach is supported by data from Isely (1932), Cole (1970), and Bacheler *et al.* (1975). Two developmental stages are modeled because of their differing microhabitats — egg through pupa in the fruit (immature stages combined) and the free-living adult stage.

Several mortality factors are represented in the model. They are (a) nonspecific density-dependent (e.g., parasitism and predation), (b) nonspecific density-independent [e.g., egg viability and a cell proliferation response of the infested square (Hinds, 1906)], (c) the effects of desiccation and temperature on immature weevils, and (d) the effects of insecticide applications on adults. Because little information is available on the nonspecific density-independent factors, their effect is assumed constant with respect to immature age. The impact of parasites on third instar larvae is described using a general approach. For example, percent parasitism is a function of larval density per acre, the maximum percent mortality attributed to the parasite when host density is not limiting, and the number of larvae at which one-half the maximum mortality is achieved.

A detailed biophysical model of square drying and associated immature weevil mortality is included in Curry *et al.* (1980). This model considers the physical changes occurring in infested fruit after abscission. While on the plant, the microhabitat within the fruit is assumed uniform. Fruit begin to dry with abscission, and the drying process is modeled as a function of fruit size, cotton variety and the condition of the microhabitat (DeMichele *et al.*, 1976). Curry *et al.* (1982) extended the bud-drying model to account for the interactions among relative humidity and temperature on immature mortality. This model describes the time required for an infested fruit of a given size to dry to a critical mass. The critical mass is defined as the minimum food needed for successful larval development. A larva must pupate before the quantity of food is reduced to the critical mass. To accomplish these tasks, development times, bud abscission times, air and soil temperatures at different locations are determined by the model. For example, temperature of infested fruit varies with fruit location (e.g., hanging on the plant after abscision or fallen to the ground) and the fraction of total daily solar radiation received at these locations (e.g., full sunlight, partial shade or full shade). Fruit that fall to the ground are distributed between and beneath plants. Other details of the crop environment are provided.

A general framework for modeling temperature-dependent stochastic longevity of adult insects is given by Curry *et al.* (1978b). Due to inadequate data for the boll weevil, this approach could not be used. Rather, longevity is estimated as 64.4 percent survival per four-day period, based on studies of Sterling and Adkisson (1970). Insecticides, when applied, kill 95 percent of the adult population.

To represent the onset of diapause, the number of non-reproductive adults in the population is based on crop phenology using a time-delay relationship between the proportion of squares and bolls attacked. For example, a cumulative normal distribution describes the proportion of non-reproductive adults in the population as a function of the proportion of eggs oviposited in bolls (relative to squares) two weeks earlier [data from Sterling and Adkisson (1978)].

Gutierrez *et al.* (1991a) — These investigators modeled the population dynamics of the boll weevil in Brazil on two long-season cotton varieties. The weevil was first reported in that country in 1981. They incorporated stochastic development of imma-

tures and adult longevity into the model of Wang *et al.* (1977). This was accomplished by using distributed maturation times to simulate populations of the weevils, cotton (Gutierrez *et al.*, 1984; 1991b), and their interactions. Details of this approach are described under the pink bollworm model of Stone and Gutierrez (1986a).

Weevils may feed multiple times on squares and bolls, but generally they deposit only one egg per square in contrast to multiple eggs per boll. Because multiple attacks may occur on a single fruit, the functional response model of Frazer and Gilbert (1976) is used to describe the number of fruit attacked due to feeding and oviposition. In this submodel, attack rates vary with (a) fruit availability corrected for weevil preference, (b) the maximum demand for feeding and oviposition sites required by the population, (c) time measured in degree-day Celsius, and (d) a weevil searching parameter that depends on plant size. Weevils emerging from bolls are assumed to be in diapause and therefore do not become reproductive. Oviposition begins when females are 285 degree-days old and end at different ages depending on the availability of squares. Insecticides are assumed to kill adults at a rate of 90 percent on the day of application, decaying to zero percent 3.5 days later.

Some interesting aspects of weevil biology are reported from Brazil that differ from those in the United States. For example, in Brazil the weevil shows only a slight preference for squares over bolls (expressed in the model as 1.1 *vs* 0.9, respectively). Fruit age (e.g., squares *vs* bolls) apparently has little effect on weevil development times in Brazil and therefore is not considered in the model. The time from weevil attack to square shed is greater in Brazil, and large squares and bolls do not abscise at all. These events may be due to the humid Brazilian conditions. They served as reasons for not modeling larval mortality due to the square drying [as found in the model of Curry *et al.* (1980)].

Process Models Not Associated With The Population Models — Several process models have been developed that are not associated with the population models discussed above. Barfield *et al.* (1977) produced a stochastic temperature-dependent model of development for the boll weevil parasite, *Bracon mellitor*. McKibben *et al.* (1982) developed a model of weevil oviposition behavior. This latter model indicates that females discriminate against squares containing an egg by rejecting as many as five punctured squares while searching for one that is pristine.

Using the boll weevil as an example, Feldman and Curry (1984) modeled temperature-dependent mortality of insects using separate rate and distribution functions. Due to the lack of data on the precise timing of weevil death, a uniform distribution is used to apportion mortality throughout the life of the immature weevil. This approach alters the predicted pattern of survivorship when compared to mortality taking place only during the emergence portion of the development period.

Stone *et al.* (1990) developed a degree-day model of spring emergence and overwinter survival of the boll weevil. Spring emergence varies as a function of the number of degree-days above 43F (6.1C) accumulated from January 1 and two indices of winter severity. These indices are used to predict overwinter survival.

Culin *et al.* (1990) and McKibben *et al.* (1991) developed models of boll weevil dispersal.

BOLLWORM, *Helicoverpa zea* (Boddie) AND TOBACCO BUDWORM, *Heliothis virescens* (F.)

These two noctuid species (members of the Noctuidae family) number among the most serious pests of agricultural crops in the Cotton Belt. They attack cotton, corn, tomatoes, soybeans, grain sorghum, alfalfa and other crops (Sterling, 1979). The worldwide importance of the *Helicoverpa/Heliothis* complex in agroecosystems was reviewed by Fitt (1989).

More than a century ago, Boddie (1850) wrote that the bollworm, better known as the corn earworm (thus the species name, *zea*), is a versatile pest which "is an anomaly in the natural history of insects." The anomaly refers to its destruction of cotton, a plant which is attacked only secondarily (that is, only when it becomes "necessary"). Bollworms overwinter 2 to 6 inches (5 to 15 cm) below the soil surface as pupae and emerge in the early spring as adults. Newly emerged moths disperse, mate and oviposit on diverse wild plants and may complete several generations before attacking cotton early in the summer. A female can oviposit from 250 to 1500 eggs during a lifespan of 3 to 12 days. The eggs are deposited on any part of the cotton plant, but tend to be placed individually in the upper third of the canopy on the upper leaf surfaces or in the terminal. Eggs hatch in three to five days, with the larvae feeding progressively on larger-sized squares and bolls for the next 12 to 15 days, molting through five to six instars before pupating. Moths emerge approximately two weeks after pupation.

The tobacco budworm was first reported as a pest on cotton in the United States in 1934, but it probably was overlooked before this time because of its close resemblance to the bollworm (Folsom, 1936). Like the bollworm, budworms are polyphagous (feed on many plants) (Neunzig, 1969). The two species have similar life cycles; however, the seasonal abundance is often dissimilar (Brazzel and Newton, 1963; Snow, 1964; Snow and Brazzel, 1965). Traditionally, budworms are more resistant to pesticides than bollworms and thus are more difficult to control.

The bollworm/tobacco budworm were among the earliest cotton insects to be modeled. Three research groups developed population models: (a) a joint USDA, ARS and Texas A&M University effort (Hartstack and Hollingsworth, 1974; Hartstack *et al.*, 1976a; Hartstack and Witz, 1983), (b) those at North Carolina State University (Stinner *et al.*, 1974a, 1977a,b), and (c) at Mississippi State University (Brown *et al.*, 1983). Their work reflects the distinct geographical and biotic differences found in each region (Fitt, 1989).

Hartstack and Hollingsworth (1974), Hartstack *et al.* (1976a), Hartstack and Witz (1983) — One of the earliest models describing cotton insects is MOTHZV. According to Hartstack and Hollingsworth (1974), this model was developed to help decide when to monitor the bollworm and budworm and when to apply chemical and biological control agents. The model is comprehensive, encompassing more than 16

subroutines including simple crop models for cotton, corn and sorghum (Hartstack and Witz, 1981a). The earliest version, MOTHZV-1, was expanded into MOTHZV-2, which represented a detailed and ambitious approach to modeling an agroecosystem (Fitt, 1989). A later version, MOTHZV-3, enhanced the cotton model and added a larval damage subroutine. A life-table approach is the bookkeeping system used by the model to account for changes in insect numbers and transitions between life-stages. For each day of the simulation, the model describes changes in the numbers of eggs, larvae, pupae, non-ovipositing adults and ovipositing adults.

In the early part of the season, MOTHZV is initialized with the number of moths caught in pheromone traps or with field counts of eggs. When used as part of the management model, TEXCIM (see below), field counts of larvae can be used to start the model. Once initialized, the model simulates the population abundance of several generations throughout the season using long-term temperature averages to drive the model. It simulates bollworm and budworm populations individually or combined. For the most part, however, the biological processes of the two species are not modeled independently.

Specific subroutines accommodate the use of pheromone trap captures as initializing values. For example, descriptive equations of trap efficiency convert trap captures into moths per acre. Another subroutine describes the influence of crop phenology (stages of plant growth and reproduction) on movement of moths between crops. For example, the predicted numbers of moths migrating out of corn or sorghum are stored for later use. Other factors include the influence of moonlight on ovipositional behavior and the impact of cloud cover on decreasing moonlight (Hartstack *et al.*, 1976a; Hartstack and Witz, 1981b).

Average temperature during the three hours after sunset is used to determine the probability of oviposition on a given night. For example, if this temperature falls between 72 and 77.9F (22.2 to 25.5C), the probability that a female will oviposit is 1.0 (100%); if the temperature falls below 55F (12.8C) or above 95F (35C), the probability is near zero. A second influence of temperature on oviposition applies a method of curve fitting, known as piecewise linear regression, to describe the effects of adult longevity (in days) on proportional daily egg production at various constant temperatures. Two additional variables influence oviposition. One determines the attractiveness of ovipositing females to other crops relative to cotton. For example, corn during silking is attractive to the bollworm but not the budworm. The other factor accounts for the proportional reduction in oviposition during periods of full moon. To obtain the total number of eggs laid per day per moth, the product of these four factors is weighted by the maximum daily egg production (set at 300 for the bollworm and 400 for the budworm).

Temperature also influences development times (in Celsius degree-days) and thus generation time from adult to adult. The lower and upper thresholds of development for eggs and larvae are 54.7F (12.6C) and 91.9F (33.3C), respectively. Eggs require 40.5 degree-days to complete development. An adjustment factor determines differences in egg development for the two species. Small larvae (first to third instar) require

81.7 degree-days, large larvae (fourth and fifth instar) require 120.6 degree-days. A nutritional factor adjusts for differences in the bollworm development feeding on cotton, corn or sorghum. The entire life cycle is completed in 484.9 degree-days. A normal distribution is used to describe developmental variability among individuals in each life stage.

Parasitism, particularly by the egg parasite, *Trichogramma* spp., is an important cause of egg mortality and is considered in the model using four options. In the first option, the number of parasites must be provided for each day of the simulation. To determine the percent parasitism to eggs, these values are used in an empirical model developed by Knipling and McGuire (1968). With the second option, daily percent parasitism must be supplied. Option three uses estimates of maximum percentage in corn for the bollworm, which is adjusted by the model as this crop matures. In the fourth option, the parasitism rate is a function of the number and age of adult *Trichogramma* spp. and of temperature. It also uses the numbers of egg predators in the Knipling and McGuire model. If ovicides are used, mortality rates are input as constants under this option. A background rate of 4.5 percent per day accounts for unexplained mortality to eggs.

Larval mortality due to predators is based on the exponential function of Knipling and McGuire (1968). A similar model (Knipling, 1971) is used to describe parasitism of small larvae. For the bollworm in corn, the number of surviving larvae is modified by cannibalism. A residual, daily mortality rate is given as four percent. Separate inputs for larval mortality resulting from insecticides are provided. As noted above, adult mortality is temperature dependent, but an additional daily rate of 15 percent is also imposed.

The cotton model SIMPLECOT [derived from a model by Wilson *et al.* (1972)] simulates the typical fruiting pattern of the plant. It describes the number of new fruit per plant per degree-day, the probability of fruit survival per degree-day, and the yield per acre. Soil type, fertility and moisture are assumed to be non-limiting. Cohorts representing the different ages of fruit are not stochastically distributed. Short, medium or long-season varieties are modeled by adjusting the parameters controlling fruiting rate. Other adjustments control different growing environments. A feedback mechanism permits regrowth of cotton (i.e., compensation) following simulated insect losses.

The damage subroutine of MOTHZV determines changes in yield caused by bollworm/tobacco budworm larvae. The numbers of small and large larvae are weighted (normalized) by their physiological age divided by 8.5. This calculation provides the "equivalent number of 8.5 day-old larvae" within the two cohort groups (e.g. small and large larvae). This weighting factor is based on data from Townsend (1973), who showed that 8.5 day-old larvae damage one fruit per day. The probability that an equivalent larva will find a square or boll is described by an exponential function of fruit density. This probability is adjusted by larval preference. For example, small larvae attack only squares, but large larvae attack both squares and bolls (with a preference for squares) depending on the proportion of bolls in the fruit population. The adjusted probabilities are used to parameterize an exponential function that calculates damaged squares and bolls per acre.

Other papers discussing improvements to and applications of MOTHZV include Hartstack and Witz (1981b), Sterling *et al.* (1989a) and Witz *et al.* (1981).

Stinner *et al.* (1974a, 1977a,b) — The modeling work in North Carolina was conducted concurrent to that of MOTHZV. Each research group provided unique contributions that complemented the other. Distinguishing features of the North Carolina model, HELSIM (HELiothis SIMulation), include intraspecific competition among bollworm/tobacco budworm larvae and the influence of patchy, small fields of mixed crop diversity on insect dynamics. The model has at least two versions: HELSIM-1 includes both the bollworm and the budworm; HELSIM-2 focuses on the impact of multiple cropping systems on population dynamics of the bollworm. HELSIM-2 makes use of contest-type intraspecific competition, and the role it plays in altering the timing of populations beyond that predicted by physiological time alone. HELSIM developers recognized that food availability sets the upper limits on insect population growth. Thus the model describes the number, type and quality of feeding sites available per hectare, as well as the spatial abundance of the principle hosts. The impact of these resources on population growth is modified by weather and natural enemies. The model uses difference equations to move individuals from one stage to the next (e.g., from one larval stage to the next, day by day), as opposed to the life-table approach of MOTHZV.

A prominent submodel of HELSIM involves the ovipositional response of the bollworm to various host plants in North Carolina (Johnson *et al.*, 1975). Four agronomic crops—cotton, corn, soybean and tobacco—are included. A spatial grid of crop types and associated crop-growth habits (up to 14 combinations) are used to simulate the movement of moths between crops (Hartstack *et al.*, 1976a). Ovipositional preference for these hosts and their spatial and temporal abundance (e.g. in relation to space and time) provides the basis for partitioning eggs among the different crops. HELSIM assumes a 1:1 sex ratio. Temperature determines the length of the pre-ovipositional period, fecundity and the temporal oviposition pattern. The data of Isely (1935) are used in describing these relationships.

Two algorithms describe development as a temperature-dependent, stochastic process. The first applies the development rates of the fastest, the median and the slowest individuals in the population held at different constant temperatures. A non-linear function is fitted to the development rate *vs* temperature data sets for the three groups of insects. Daily field temperatures are used to drive the three rate equations independently, and the predicted rates are summed to unity (1.0) to determine development times. Thus, a rate-summation approach is used to predict the development times of three different portions of the population. A cumulative distribution is then fitted to the three predicted development times plotted against their respective proportion of the population. Data of Isely (1935) are used to parameterize the larval development submodel. Other data on local insect strains and conditions are used for its validation.

HELSIM provides greater detail on larval cannibalism than does MOTHZV. In fact, cannibalism is the dominant mortality factor when larvae are found on corn. The cannibalism subroutine calculates the spatial distribution of larvae among ears of corn. This subroutine determines the probability that a larva will come into contact with

another at the same site. Cannibalism occurs when more than one larva is found at a given site. When high population densities are present, cannibalism alters survival and the timing of generation peaks. Generation times can be reduced up to 18 percent by this factor because older larvae can eliminate large proportions of small larvae that hatch from eggs oviposited later.

The abundance of natural enemies varies according to host-plant type and its phenological state. This effect tends to dampen density-dependent numerical responses and alters the functional response of natural enemy populations. Because bollworm/tobacco budworm moth populations disperse, there is a temporary release of insect populations from natural control. While these and other influences are recognized in HELSIM, they are simply lumped into a value that describes daily mortality as function of crop type, maturity and time.

The work in North Carolina motivated several innovations that not only improved HELSIM but also had broader applications to other insects. The first of these innovations involves the use of non-linear functions to describe temperature-dependent development rates (Stinner *et al.*, 1974b). Later improvements incorporated developmental variability among individuals in the population (Stinner *et al.*, 1975). These algorithms may have been the first applications of a non-linear, stochastic approach to modeling insect development in population models. Another innovation is the descriptive model that predicts the spring emergence of bollworm populations in North Carolina (Logan *et al.*, 1979). The emergence model includes the effects of soil type as well as the interactions between soil type, temperature and soil moisture in influencing the post-diapause development and survival of overwintering pupae. This work influenced the development of an expert system for building pest simulation models (Logan, 1988).

Brown *et al.* (1983) — An initial bollworm/tobacco budworm model called HELSYS (Harris *et al.*, 1976) was developed by the Mississippi group; however, changes in personnel led to the abandonment of this model. Later work produced an alternative model, CIM-HEL (Cotton and Insect Management-Heliothis), which built upon MOTHZV and to a lesser extent HELSIM. CIM-HEL emphasizes bollworm/tobacco budworm feeding on cotton, with larval preferences for fruiting forms derived from studies by Wilson and Gutierrez (1980) and Nicholson (1975). The detailed approach to larval feeding, along with the use of the boll weevil model of Jones *et al.* (1975a,b, 1977) and the cotton model, COTCROP (Jones *et al.*, 1980), led to the development of the management model, CIM (see below).

Unlike MOTHZV which separates the two species only when necessary (Hartstack *et al.*, 1976a), CIM-HEL models each species individually. According to the Mississippi group, separation of the two species is justified because of their significant differences in development, fecundity and resistance to insecticides. CIM-HEL uses discrete time-steps in degree-days; however, the output of the model is given in calendar (Julian) days. Bookkeeping on the number of individuals per life stage and the timing of life stage transitions is performed using a Leslie matrix approach.

CIM-HEL is initialized using the numbers of insects in each life stage, or alternatively, the numbers of adults entering the field in the spring (Murphey, 1980). The model applies the fecundity subroutine of MOTHZV without its moon-phase effect (Murphey, 1980). Development is temperature-dependent using the linear, degree-day approach (measured on a Celsius scale). Developmental variability among individuals is also simulated. Eggs require 50 degree-days to hatch. Data on larval development are obtained from Hogg and Calderon (1981), with the bollworm requiring slightly longer to develop than the budworm (310 *vs* 300 degree-days, respectively). Female pupae of both species develop faster than males; however, because only females influence population growth (Hogg and Gutierrez, 1980), their rates alone are used in the model. Pupae of both species develop in about 235 degree-days.

Egg and larval mortality result from predators, other natural causes and insecticide applications. The predator/parasite population is not modeled explicitly but, on occasion, very simple population models for predators/ parasites are used (Brown *et al.*, 1979a). The numbers for predators/parasites are supplied from field samples as an exogenous variable (Brown *et al.*, 1979a; McClendon and Brown, 1983). Therefore, egg and larval mortality are proportional to the numbers of predators/parasites supplied. CIM-HEL models the recovery of predator/parasite populations following an insecticide application. This task is done using a step function that has an 80 percent decrease in their numbers on the day of application. A linear function is used to describe their recovery rate over a 14-day period.

Larval mortality due to insecticides is based upon a table of supplied values that describe daily mortality for each larval stage (first to sixth instar). The values differ for each species. Larval mortality from insecticides on the day of application decreases from about 95 percent for first instar to less than six percent for sixth instar. Daily mortalities by instar are reduced on the second and third days post-application to simulate residual insecticide mortality. Additional daily mortalities are three percent for eggs and pupae and 15 percent for adults. Data from Hogg and Nordheim (1983) are used to parameterize larval survival rates in CIM-HEL.

Empirical relationships are used to describe and couple the feeding behavior of bollworm/tobacco budworm with the Cotton Crop Model, COTCROP (Brown *et al.*, 1979b). This crop model was derived from SIMCOT II specifically for interfacing with insect models. Unlike SIMPLECOT used in MOTHZV, COTCROP is a detailed process-oriented, physiological plant model. Growth rates of plant organs depend on temperature, age and the availability of carbohydrate and nitrogen reserves. This modeling capability permits the comparison of crop practices such as irrigation and fertilization to insect management tactics. Conforming to other IPM modeling groups, Mississippi researchers held to the view that "one must vary the number of fruit ... per area in a continuous manner" in order to model insect feeding on cotton (Brown *et al.*, 1983). Thus, COTCROP simulates the growth of plants in one square meter areas, rather than the average plant. The number of fruit eaten per day per larva is a linear function of larval age. Larval fruit preference is influenced by both fruit and larval age.

The estimate of feeding damage is stored in an array so that the cotton model can appropriately schedule the abscission date of damaged fruit.

Process Models Not Associated With The Population Models — HELDMG (HELiothis DaMaGe) (Thomas, 1989a,b) is a bollworm/tobacco budworm damage model coupled to the cotton model, GOSSYM (Baker *et al.*, 1983). This model also uses the damage function from MOTHZV (Hartstack and Witz, 1983), and the larval fruit-preference equations of Wilson and Gutierrez (1980). Using inputs from either scouting reports or MOTHZV (as part of TEXCIM), HELDMG simulates the within-plant distribution of larval damage. The model apportions the projected number of damaged fruit on the plant in order to adjust the fruit distribution of GOSSYM. Thus, a platform is provided that can be used to study the effects of larval damage on cotton growth and yield. Explicit management options for bollworm/tobacco budworm control are not specified; rather, the user has to decide if the forecast of bollworm/tobacco budworm damage is severe enough to take action.

Other models include: (a) a regression equation describing the population buildup of bollworms (Butler *et al.*, 1974), (b) a sex pheromone emission model (Hartstack *et al.*, 1976b), (c) genetic suppression models of the tobacco budworm (Makela and Huettel, 1979; Levins *et al.*, 1981; Roush and Schneider, 1985), (d) a distribution model of bollworm development times (Sharpe *et al.*, 1981), (e) a damage reduction model of bollworm/tobacco budworm on cotton (Young and Wilson, 1984) and (f) an emergence model for overwintering bollworm/tobacco budworm (McCann *et al.*, 1989).

COTTON FLEAHOPPER, *Pseudatomoscelis seriatus* (Reuter)

The fleahopper is a key pest of cotton in Texas and adjoining states. The insect is polyphagous (feeds on multiple plants) and multivoltine (more than one generation per year), with five to eight generations per year. It overwinters as diapausing eggs, which often are found in the fall on stems of the wild host, wooly croton, *Croton capitatus* Michx. Eggs begin to hatch on warm spring days and continue do so for up to two months. Rainfall triggers egg hatch. Typically, the first two generations are found on wild hosts, with adults of the second generation moving to cotton after the preferred hosts senesce.

Proper management of this insect is important for several reasons. While on cotton, it feeds on pinhead squares causing them to abort. Poorly-timed insecticide applications against the insect can release other pests from natural control, resulting in additional losses in production and increases in control costs. The fleahopper is an important predator of bollworm/tobacco budworm eggs, and is a food source for polyphagous predators, particularly spiders (Hartstack and Sterling, 1986). These last two characteristics make modeling this insect unique in comparison to other cotton insects. One population model developed at Texas A&M University exists for the species (Hartstack and Sterling, 1986).

Hartstack and Sterling (1986) — The Texas cotton fleahopper model predicts fleahopper abundance through time and cotton fruit losses caused by the insect. These

forecasts are designed to help producers make management decisions on fleahopper control. The model can stand alone or be used as part of the comprehensive management model, TEXCIM (see below). The fleahopper model is coupled to the cotton model, SIMPLECOT, which assigns fruit to cohorts according to their physiological age. Temperature and rainfall are the principle variables affecting fleahopper diapause, spring emergence, development and oviposition.

The model simulates the number of eggs entering diapause in the fall as a function of calendar date. The probability of diapause is described by a linear function, with no eggs entering diapause before September 1 and all eggs entering after October 11. Temperature and rainfall are used to estimate the timing of spring emergence. The emergence pattern of nymphs provides one approach for initializing the fleahopper population model. The number of nymphs observed in a field provide an alternative approach. Using these inputs, the model predicts changes in population density through time for the F_1 and subsequent generations.

A degree-day approach is used to predict development times of eggs and nymphs as a function of temperature. The lower threshold of development is 58.2F (14.6C) and the upper threshold is 92F (33.3C) (Sterling and Hartstack, 1979). This approach is integrated with the distribution method of Sharpe *et al.* (1977) to determine developmental variability among individuals in the population. The model uses "physiological days" as the basic time step, which are defined as the degree-days (Celsius) per calendar day divided by 13.3 degree-days. The development times of eggs and nymphs are 9 and 7.2 physiological days, respectively.

Females oviposit a maximum of 20 eggs per day, depending on temperature and female age. Eggs are oviposited between 62.6F (17C) and 95F (35C). Females are reproductive during the ages of 1.6 and 13.5 physiological days. If female age is between 3.5 to 6.09, the probability of oviposition is 1.0 (100%). For ages <3.5 or >6.09, the probability of oviposition is determined by two linear functions, one for each interval. The sex ratio of adults is set at 0.5.

To indicate potential insect problems, fleahopper abundance through time is compared to the fruiting curves provided by SIMPLECOT. The damage rate of both nymphs and adults is 0.5 squares per day for squares younger than five days. Older squares are not damaged. An exponential function is used to estimate the number of damaged squares per day as a function of insect numbers and the density of susceptible fruit. This damage function is similar to that used by MOTHZV to describe bollworm/tobacco budworm damage (Hartstack and Witz, 1983).

The number of fleahopper nymphs dying each day is temperature- and age-dependent. Mortality increases when temperatures are above 84.9F (29.4C) or below 75F (23.9C) (Gaylor and Sterling, 1975). Adult mortality increases with temperature and physiological age. Adults live 376 degree-days (or about 28 physiological days).

Mortality by insecticides is determined by a table of values. These mortality values range from 5 to 20 percent for eggs, 90 to 99 percent for nymphs, and 70 to 99 percent for adults. A residual effectiveness of each insecticide, typically less than 4.3 days, is also provided. The type of insecticide, the number of applications and the day of appli-

cations are specified before the population model is run. The mortality rate due to the various insecticides are estimates and caution is recommended in their use. The nymph and adult insecticide mortality rates are modified by the aging process.

Fleahopper mortality is also dependent upon field counts of the numbers and types of fleahopper predators. The efficiency of each predator group is weighted, with spiders given the most weight. If field samples are not available, default predator levels and types can be selected, along with default estimates of the timing of natural enemy abundance. The predation rate is based upon the predator model of Knipling and McGuire (1968). The maximum daily predation rate of eggs and nymphs is five percent.

PINK BOLLWORM, *Pectinophora gossypiella* (Saunders)

The pink bollworm is not native to North America but was introduced into Mexico in 1911 and spread to the United States in 1916. Presently, it is found in cotton growing areas west of the Mississippi River, where it is a pest in Arizona and California. The insect is confined to malvaceous plants; cotton and okra are the only two cultivated crops in the United States attacked. Adults are small moths (Microlepidoptera) that are active in the predawn hours. Females release pheromones to attract males. Bolls are the preferred oviposition (egg-laying) site, but prior to bloom, eggs may be found on all plant parts. Development occurs within a single fruit. Generally only one larva survives per square, but several can survive in a single boll. Feeding in squares is directed to the anthers, whereas in bolls preference is shown to lint and seeds. Pupation occurs in the soil or in lint, and pupal mortality can be high from extremes in soil temperature or moisture. The insect overwinters as a mature larva in the soil or in dried bolls.

Population models have been developed by Larson and Huber (1975), Gutierrez *et al.* (1977a), Stone and Gutierrez (1986a), and Hutchison (Unpublished manuscript, W. D. Hutchison, Department of Entomology, University of Minnesota, St. Paul, MN). Larson and Huber (1975) adapted the western lygus bug, *Lygus hesperus* Knight, model of Watson (1973) to pink bollworm. This model does not explain the mechanisms behind process-level events, but is purely descriptive.

Gutierrez *et al.* (1977a) — Gutierrez *et al.* (1977a) developed a detailed model using a von Foerster (1959) approach to represent the population of pink bollworm. The model calculates the age structure of the population in degree-days Celsius and applies a complex net mortality function that depends on age, time, density, temperature and the net immigration-emigration rate of adults into the population. At any point in time, the population consists of adults emerging from diapause, eggs, larvae, pupae and adults emerging from squares or bolls.

The model describes cumulative percent emergence of adults from diapause using Gompertz equations fitted to the field data of Rice and Reynolds (1971). Oviposition rates vary with female age, with more eggs deposited earlier in the adult life than later. Maximum fecundity (egg-laying capability) is 240 but the actual value per female

depends on the nutritional history of the insect. For example, the fecundity of females emerging from diapause is scaled by 0.66. Scaling factors of 0.8 and 1.0 are given to females that fed on squares and bolls as larvae, respectively.

Accumulated degree-days above 50F (10C) (Butler and Hamilton, 1976) are used to calculate the development times under fluctuating temperatures. The field data of McLaughlin (1974) provided estimates of the range of development for each life stage: eggs from 0 to 83 degree-days (in Celsius), larvae from 83 to 233 degree-days, pupae 233 to 450 degree-days, pre-reproductive adults 450 to 478 degree-days, and adults 478 to 794 degree-days, respectively. This was verified in the laboratory on artificial diet. Fruit age, determined by their cotton model (Gutierrez *et al.*, 1975, Wang *et al.*, 1977), influences food selection as well as development rates of newly emerged larvae. For example, larvae show little preference for very young squares, bolls or flowers. A square supports only one larva, while a boll supports up to 15. Development rates vary with age of the fruiting structure using scalars that adjust degree-days accumulation (Lukefahr, 1962).

Temperature and photoperiod influence diapause initiation of pink bollworm (Albertos, 1974). These factors are used to calculate the percentage of first instar larvae that go into diapause. Individuals that go into diapause are treated as emigrants in the population since they do not develop beyond the prepupal stage.

Mortality factors are described for various life stages. Predators reduce eggs and newly hatched larvae by five percent on bolls and 15 percent on foliage. Only 82 and 92 percent of newly emerged larvae locate squares or bolls, respectively, on which to feed. Once the fruit is attacked, pink bollworm larvae are immune to predator attack. Adults die in an age-dependent manner.

Data from Brazzel and Gaines (1956) are used to describe pink bollworm damage to cotton. Percentage loss of lint, seeds, and reduced quality are described as exponential functions of the number of larvae per boll (details of these submodels are not provided by the authors).

Stone and Gutierrez (1986a) — These investigators modified the pink bollworm model of Gutierrez *et al.* (1977a) in two significant ways. First, they incorporated developmental variability among individuals into the model (stochastic development) for both cotton and pink bollworm. For example, fruit of a given cohort ages according to a Gamma probability density function describing the mean and variance of development times. This function is also used to describe the probability of pink bollworm completing development, applying the constant temperature data of Hutchison *et al.* (1986) to parameterize the model for each larval stage. The model also enhances the nutritional influence of the host on larval development. Instead of incorporating nutrition as a correction factor for the aging process (Gutierrez *et al.*, 1977a), Stone and Gutierrez (1986a) expanded the concept of physiological time to include the nutritional influences of the host on pink bollworm development. The nutritional value of the fruit (represented as a scaling multiplier for developmental rate of the infesting larva) varies as a continuous function of fruit age (measured in degree-days). Thus, the

aging rate of a larva at any particular time not only depends on temperature but also on the nutritional value of the fruit.

Hutchison (Unpublished manuscript, W. D. Hutchison, Department of Entomology, University of Minnesota, St. Paul, MN) — Hutchison used the degree-day approach to describe the mean development time of pink bollworm life-stages and the distribution approach of Logan (1988) to describe the variation in individual development times. The data of Hutchison *et al.* (1986) are used to parameterize the models (with lower and upper threshold values of 51.6 and 90.5F [10.9 and 32.5C]). The data of McLaughlin (1974) are used to validate the models. A logistic equation describes cumulative oviposition as a function of physiological age (in degree-days). The maximum fecundity of females varies with nutrition according to the formula used by Gutierrez *et al.* (1977a). Unlike other pink bollworm models, this model describes the probabilities of a time delay in oviposition attributable to sublethal dosages of three insecticides (using data of Hutchison *et al.*, 1988).

Process Models Not Associated With The Population Models — Butler and Hamilton (1976) used the function of Stinner *et al.* (1974b) to model pink bollworm larval and pupal development as a function of temperature. Butler and Watson (1980) developed a model that estimates daily survival of adults as a function of temperature. Gutierrez *et al.* (1981) improved the diapause induction and spring emergence models proposed in their earlier work (Gutierrez *et al.*, 1977a). Their analysis showed that the environment experienced by individuals at the time of diapause induction and spring emergence influences the combined pattern of adult emergence in the spring.

TARNISHED PLANT BUG, *Lygus lineolaris* (Palisot de Beauvois), AND WESTERN PLANT BUG, *Lygus hesperus* (Knight)

Plant bugs are polyphagous (feed on many plant species), multivoltine insects found on a wide variety of agronomic crops and weed species. The tarnished plant bug, *Lygus lineolaris*, is widely distributed throughout North America, occurring on cotton from the Carolinas to Texas. *Lygus hesperus* (western plant bug) is found in the West, primarily in Arizona and California. Cotton is not a preferred host of either species, but adults migrate into this crop after the primary hosts have matured, died out, or are harvested. In the East, *Lygus* spp. typically develop large populations on early-season annuals; in the West, alfalfa and safflower are reserve crops. Young squares that are attacked will abort, but loss of older fruit is uncommon. The pest status of these species is debated. Some studies show that common densities observed in cotton do not reduce yields or quality (Falcon *et al.*, 1971; Gutierrez *et al.*, 1975). However, large migrating populations can cause severe damage (Gutierrez *et al.*, 1977b).

A population model of the tarnished plant bug in cotton and a wild host was developed by Fleischer and Gaylor (1988). Watson (1973) and Gutierrez *et al.* (1979b) modeled the western plant bug in cotton (the Watson model was not available for review). Gutierrez *et al.* (1977b) developed a population model for the western lygus bug in alfalfa.

Fleischer and Gaylor (1988) — These investigators studied nymphal development and survival, and adult longevity and fecundity of the tarnished plant bug on several hosts including cotton. A Leslie matrix approach is used to model the insect on cotton and the wild host annual fleabane, *Erigeron annuus* (L.). This model describes a population of individuals of differing age classes; each age class has a reproductive rate and a probability of surviving to the next class. The dynamics of the model are determined iteratively (repetitively) according to a matrix equation, whereby the age distribution of individuals at any time is a function of time, varying birth rates and death rates. The model is parameterized using life-table data collected in the laboratory at 79.7F (26.5C). This simple model indicates greater population growth of the tarnished plant bug on annual fleabane than on cotton. The model is not integrated with a model of the host.

Gutierrez *et al.* (1979b) — These researchers simplified the western plant bug model of Gutierrez *et al.* (1977b), which applied a matrix approach similar to that of Fleischer and Gaylor (1988). The model does not consider reproduction, development or other life processes explicitly, or the mechanisms that influence these processes. Rather, it uses two empirical functions to describe field observations. For example, they found that the number of western plant bug adults in standard sweepnet samples increases exponentially with the number of cotton squares in the field. To adjust for sweepnet inaccuracies, the predicted number of adults given by this function is multiplied by 3.65 (after Byerly *et al.*, 1978). Using the fruiting subroutines of their cotton model (Gutierrez *et al.*, 1975; Wang *et al.*, 1977), the number of adults through time is estimated as a function of available squares. The number of nymphs in the population is a function of the number of adults, given a 200 presumed degree-days Fahrenheit time delay for egg development. Development time of eggs is estimated as 200 degree-days above 53.5F (11.9C), and the time for nymphs is 400 degree-days. The net immigration rate into cotton is a constant, set at 0.01.

Insecticides presumably kill all plant bugs at the time of application. After application, it takes 200 degree-days for adults to reinfest the field. Between 200-800 degree-days, the rate of increase for adults is 1.4 times normal due to a suppressed natural enemy complex. Nymphs also benefit from the decline in natural enemies after a spray, increasing 2.27 times the norm.

Plant bugs injure small squares, with adult females causing about twice as much damage as males. The average rate is 0.028 squares per degree-day for females *vs* 0.0134 for males (Gutierrez *et al.*, 1977b). According to the investigators, the injury resulting from nymphs occurs at a rate of 0.0142 squares per degree-day. These results contradict the belief that nymphs cause twice the damage as adults.

Process Models Not Associated With The Population Models — Fleischer and Gaylor (1988) used linear models to describe development rates as a function of temperature for the tarnished plant bug nymphs reared on nine hosts, including cotton. No significant differences in the slopes or intercepts of these equations are found. This suggests that a single model fitted to the pooled data may represent development adequately on all hosts.

Butler and Wardecker (1971) modeled the western lygus bug development rates as a function of temperature using a linear model. Strong (1971) simulated the mating behavior of the insect on alfalfa. Mangel *et al.* (1985) applied analytical methods to examine changes in the numbers of squares and western lygus bug in the field through time. Although there was an inverse correlation between squares and western lygus bug numbers during certain weeks of squaring, no evidence is presented supporting their assumption that the relationship was due to the insect.

SPIDER MITES, *Tetranychus* spp.

Three mite species attack cotton in the United States. In the West, where mites rank among the most important arthropod pests, the strawberry spider mite, *Tetranychus turkestani* Ugarov & Nikolski, occurs chiefly in the early season; the twospotted spider mite, *Tetranychus urticae* Koch, occurs in the mid-season; and, the Pacific spider mite, *Tetranychus pacificus* McGregor, dominates during the late season. In most areas outside the West, outbreaks of the twospotted spider mite occur chiefly during dry summers. Mites damage the plant through leaf feeding and by injecting phytotoxins which affect stomatal conductance, leaf resistance, transpiration and net photosynthesis (Marcano, 1980).

We are not aware of any population models for spider mites in cotton. Wilson *et al.* (1985) developed a spider mite forecasting model that determines sampling times and cotton damage potentials. This model is integrated into a rule-based expert system, CALEX, for making pest management decisions in California (see below).

MODEL APPLICATIONS

Population models have been used for understanding and describing the cotton/insect system and, to a limited degree, for managing it. We discuss general applications followed by specific instances and case studies.

GENERAL APPLICATIONS

Initial steps in the modeling process are to define the boundaries of the system under study and identify the components and their interactions that are essential to its operation. In this way, a mental or conceptual picture is formed of how the system works, or how we believe it works. These steps provide organization, structure and direction to research. They help to: (a) identify important topics for study, (b) assemble known information on each topic, (c) determine where the information fits in the scheme of things, and (d) determine what should be done next. Therefore, the modeling process focuses research on relevant questions about the nature and behavior of the system. This value does not change once the model is formulated. It then becomes a powerful tool for directing research through sensitivity analysis, which helps identify the components (parameters) that must be measured with greatest precision.

Models can be used to test scientific hypotheses, an application with relevance to management as well. For example, many of the simulation models developed from the

IPM projects provide a method for devising and evaluating effective management strategies or for evaluating the potential pest status of a species (examples are provided below). The tasks of devising and evaluating new strategies are useful only if the strategies can be implemented, and models provide a method for accomplishing this task as well. As we will examine later in this chapter, computer-based systems provide an excellent way to implement comprehensive crop/pest management strategies. New strategies can be very complex, and even experts have difficulty evaluating the agroecosystem as a whole. All management options may not be known, and the changing nature of events in the field are not always straightforward or intuitive. Computer-based systems have the power to integrate, analyze, interpret, hypothesize and deliver complex information on the important components of the agroecosystem. These components include crop dynamics, pest population dynamics, treatment tactics, impacts and cost/benefit analyses.

Models can promote the effective use of agricultural chemicals through proper timing of applications and by recommending the most efficient products (or combination of products) and dosage rates. This use of models should reduce pest resistance problems and extend product durability and efficacy. Concurrently, alternative methods of control with less economic and environmental impact should become viable options that can be used with greater confidence (less risk). Models may be used to develop and test potential new agricultural products, such as some of the genetically-altered new cotton varieties (e.g., those containing a *Bacillus thuringiensis* protein effective against lepidopterous pests). They can provide a concise summary of the proposed mode-of-action of a tactic or strategy, and then be used to evaluate the tactic before costly field evaluations are initiated.

SPECIFIC APPLICATIONS

Some of the comprehensive simulation models described in this chapter have been well tested and provide good descriptions of the biological systems they represent. For these reasons, they have been used to evaluate management strategies consistent with IPM objectives — to improve crop production and reduce pest damage by augmenting natural enemy populations, using host-plant resistance and cultural modifications, and by evaluating a species' pest status or dynamic spray thresholds. Other models address what Newsom (1980) called "The next rung up the ladder", which involves the management of multiple pest species that occur simultaneously. While these "mega-models" represent progress, much work remains. As noted by Gutierrez and Wilson (1989), the development of management models in cotton is a recent event; one that could only take place after the models accurately represent several sets of independent field data. This validation process is not easy, for often time-consuming experiments reveal gaps in our understanding of biological relationships.

CIM (Cotton and Insect Management) — Mississippi scientists developed the cotton crop model, COTCROP (Jones *et al.*, 1980), integrating it with simplified versions of the bollworm/tobacco budworm and boll weevil models (Brown *et al.*, 1983;

Jones *et al.*, 1977), yielding a comprehensive tool for managing insects primarily through insecticides (Brown *et al.*, 1983). CIM simulates the daily changes in the crop and insects from crop emergence to harvest. Initial insect densities of both pests and predators are supplied by the user. Other model inputs include soil characteristics, date of crop emergence and harvest, plant population density, nitrogen and insecticide applications and daily weather data. Model outputs include daily records on the crop, insect densities by life stage, and a summary report provided at the end of the simulated growing season. This report includes the yield estimate, the number and cost of insecticide applications and the net dollar return (Brown and McClendon, 1982; Brown *et al.*, 1983). By varying the historical weather data, soil types and insect densities, different insect management strategies can be evaluated.

CIM was developed specifically for devising, evaluating and improving insect management strategies in Mississippi (McClendon and Brown, 1983; Murphey, 1980). For example, using simulation and field results, researchers developed a dynamic threshold strategy for managing small bollworm/tobacco budworm larvae. This concept was tested against the recommended threshold of the time (1979). The dynamic threshold varied with the changing status of the crop. The results indicated that the dynamic threshold could reduce the number of insecticide applications without a loss in yield, thereby increasing profits. In general, insecticides were applied earlier using this threshold, and late-season applications were avoided for fruit that would not mature.

Besides its use in developing management strategies, CIM has a specialized application as a teaching aid in the model COTGAME (Pieters *et al.*, 1981). Presently, CIM is not widely used in production systems due to the lack of a user-friendly interface, documentation and training of potential users.

Curry *et al.* (1980) — The Texas cotton/boll weevil model of Curry *et al.* (1980) is comprehensive and well-tested and provides good biological descriptions of the system. It was used to evaluate pest management strategies consistent with IPM objectives. For example, the model was used to investigate a variable treatment-level threshold for the boll weevil similar to the dynamic threshold described above. The variable treatment-level threshold gives priority to early-season fruit and decreases protection for late fruit (Curry and Cate, 1984). This approach adjusts treatment levels according to the following schedule: one percent damaged buds until first bloom, 25 percent until first 12-day-old bolls and 75 percent for the remainder of the season. Simulation analysis indicated that the variable treatment-level threshold improved control with fewer treatments, increased cotton yields and reduced the possibility of secondary pest outbreaks when compared to the standard 10 percent punctured-square threshold or the approach proposed by Walker and Niles (1971). The last approach calls for three applications at four-day intervals starting with the occurrence of one-third grown squares.

Curry and Cate (1984) also used the model to evaluate the impact of natural enemies compared to insecticide control, both alone and in combination with a 20 percent decrease in weevil development rates resulting from hypothetically altered host resistance. In the former case, natural enemies provide less control than insecticides; in the

latter, the combined effects produced excellent control without the use of insecticides. Additional model analyses examined combinations of other possible benefits resulting from altered host resistance, e.g., decreases in reproductive rates and increases in mortality rates of the weevil.

In an optimization study using the model, an economic analysis was conducted of multiple insecticide applications directed at the weevil in the absence of bollworm/tobacco budworm (Talpaz *et al.*, 1978). The analysis used a cumulative Weibull function to determine kill rates as a function of insecticide amounts. The results indicated that insecticide applications should be timed to coincide with critical windows during the development of the crop. Dosage rates, however, are sensitive to price changes in insecticide and cotton.

DEMHELIC (DEcision Model for HELiothis In Cotton) — This model collates information from diverse sources (Brown *et al.*, 1983; Gutierrez *et al.*, 1975; Hartstack *et al.*, 1976a, 1982; Hartstack and Witz, 1983; Room, 1979; Stinner *et al.*, 1974a; and Wang *et al.*, 1977) into a decision tool for bollworm/ tobacco budworm management (Hopper and Stark, 1987). It emphasizes the use of natural enemies as opposed to insecticides which disrupt natural enemy populations. A secondary objective is to minimize other negative influences of insecticide use, such as pollution, pest resurgence and secondary pest outbreaks. It does not employ population models *per se*.

A distinguishing feature of DEMHELIC is the use of small spatial (of or relating to space) and short temporal (of or relating to time) horizons. For example, the authors maintain that the spatial variation in bollworm/tobacco budworm populations is too great to permit accurate predictions within fields. This view is in contrast to that adopted by TEXCIM. Model corrections are made weekly or twice weekly using scouting data from the field. These brief horizons are also used because the effects of current management practices on bollworm/tobacco budworm populations and natural enemies are not well understood. For these reasons, DEMHELIC makes extensive use of sampling data on predator/parasite density, bollworm/tobacco budworm density and feeding damage, cotton growth patterns and weather. The program provides ranked management options to the user.

Gutierrez *et al.* (1979b) — Using optimization procedures with simulation results, these investigators analyzed the impact of western lygus bug on Acala cotton yields in California, both with and without the use of pesticides. Their results indicated that the insect is not a pest of cotton under most circumstances; rather, it often enhances yields. Yield enhancements occur because only very young squares are shed after injury from lygus, and this loss causes minimal impairment of the plant's ability to compensate. Pesticide applications against the insect reduced yields rather than increasing them. Reduced yields in combination with the cost of treatment lowered profits compared to simulation results with no treatment. The use of pesticides against lygus may also cause a resurgence of secondary pest species after the destruction of beneficials. In some cases, significant injury and economic losses can occur when large numbers of the western lygus bug migrate into cotton from cut hay.

Gutierrez *et al.* (1991a) — Using simulation analysis, Gutierrez *et al.* (1991a) examined the impact of the boll weevil on long-season Brazilian cottons compared to a short-season Texas variety. The analysis indicated that Brazilian cottons do not compensate as well for fruit losses due to nitrogen stress or the weevil. Instead, they allocate more photosynthate to vegetative growth rather than new fruit production. The Texas variety, bred to avoid weevil damage, produces greater yields than the Brazilian cotton because of its greater fruiting rate (which allows for the replacement of some shed squares), lower loss rate per fruit (fruit are smaller in size) and faster maturation times. The investigators concluded that cottons bred for maximum compensation for the boll weevil should require less insecticide for weevil control and return greater profits.

Stone and Gutierrez (1986b) — These investigators developed a management model for the pink bollworm by integrating pesticide and pheromone (gossyplure) routines into their cotton/pink bollworm model (Stone and Gutierrez, 1986a). The pesticide submodel assumes a maximum kill (to all adults and eggs on the foliage) at the time of the application; thereafter, the death rate decreases exponentially with time. The pheromone submodel reduces mating by applying gossyplure from discrete point sources (emitting devices). The number of active sources in the field depends on the number applied per acre (a model input), the loss rate of sources that drop off plants (a function of degree-days since application), and the number of applied sources that adhere to the foliage (a scalar computed from the cotton model output). The release rate of pheromone per unit area is described as an exponential decay curve. If the concentration of pheromone is above a minimum threshold, no mating occurs; if it is below the threshold, the effectiveness of the pheromone in reducing mating is a ratio of the actual concentration to the lower threshold.

Using the model, Stone *et al.* (1986) analyzed the economics of pheromone use for pink bollworm control, compared to and in conjunction with insecticides. This analysis indicated that early-season use of pheromones in combination with insecticides applied at low thresholds is the most profitable, especially at low pink bollworm population densities. The model has been used in the Palo Verde Valley of California (Gutierrez and Wilson, 1989).

TEXCIM (TEXas Cotton Insect Model) — TEXCIM (Sterling *et al.*, 1992) is a comprehensive collection of cotton insect and crop simulation models joined to an economic assessment package (also see Chapter 7, this book). A primary function of this integrated program is to provide crop managers with sound economic advice for making pest control decisions. This task is accomplished by comparing the costs and benefits of controlling multiple pest species over the duration of a growing season on a field-by-field basis. The program has undergone five revisions, each adding greater functionality through new or altered components, improved robustness through broader validation, and ease-of-use through editors, charts, and a windowing environment. Originally designed for use in Texas (available through the Texas Agricultural Extension Service), cooperators are now located in different cotton growing states and in several foreign countries. The present release (version 5.0) contains insect simulation models for the cotton fleahopper (Hartstack and Sterling, 1986), bollworm

(Hartstack *et al.*, 1976a), boll weevil (Curry *et al.*, 1980) and pink bollworm (Gutierrez *et al.*, 1977). It uses the plant model, SIMPLECOT (Wilson *et al.*, 1972).

The manner and extent to which TEXCIM has adapted and applied extant simulation models is unique in cotton. The integration of individual simulation models, developed by numerous researchers during the 1970s and 1980s, is not a trivial task. As summarized in this chapter, these models are often large and detailed. For this reason, such a consolidation will likely not be duplicated. Rather, TEXCIM may ultimately find additional value as part of other computer-based management systems presently under development. One such cooperative effort involves another Texas research group, in which TEXCIM is being linked to a newer model, Integrated Crop Ecosystem Management Model, ICEMM (Benedict *et al.*, 1991; Landivar *et al.*, 1991). ICEMM contains the crop simulation model, TEXCOT, which is a modification of GOSSYM (Baker *et al.*, 1983). Unlike SIMPLECOT, TEXCOT is a physiologically-based model that accounts for photosynthetic production and allocation. This foundation provides greater realism to the cotton model and allows linkage to models of other herbivore pests such as sucking insects. For example, simulation models for the cotton aphid (Xie and Sterling, 1987) and sweetpotato whitefly (von Arx *et al.*, 1983) now reside in the integrated system. Also, the original bollworm model in TEXCIM has been modified to form a new tobacco budworm model. TEXCIM/ICEMM provides expanded advice on economically optimal crop management with regard to insecticides, fertilizers, irrigation, and plant growth regulators. It accomplishes this task by estimating the costs of these agronomic inputs, as well as the costs of consultants, insurance, interest, pest resurgence, pest resistance, on-farm health and environmental effects. These costs are compared to potential benefits derived from the use of the input(s), and if benefits exceed costs, the program recommends application.

REASONS FOR LACK OF FARM USE OF POPULATION MODELS

A vast amount of knowledge on agricultural systems came out of the research efforts of the 1970s and early 1980s, and much of this knowledge is summarized in the cotton crop/pest models. Despite the emphasis on implementing alternative management practices, most IPM models have not been used beyond their original research roles. With few exceptions, this research effort has served agro-management only indirectly. The application of population models to problem solving at the farm level was not fully realized for several reasons. We discuss below reasons specific to cotton. Coulson *et al.* (1990a) defined the problems associated with the development and operation of computer-based systems in forest pest management, which are similar to those encountered in agricultural systems.

Pyrethroids were introduced commercially into cotton in 1978. As this group of new compounds became more available and cost-effective over the next several years, the liberal use of insecticides was reinstated as the primary means of pest control. This result diminished the urgency to develop and apply alternative management strategies during the early 1980s. It was apparent that as long as insecticides remained practical, efforts to integrate pest management models into agriculture would be difficult.

By 1985, the "Huffaker and CIPM" projects that supported the research and development of the IPM models ended. Interdisciplinary teams conducting the research had recruited and retained excellent people during the tenure of these projects. However, without national backing, the administrative and financial support needed to preserve project continuity was lost. Many projects could not maintain adequate funding, resulting in their partial or entire disbandment. Accumulated knowledge, expertise and the momentum to accomplish the overall objectives were lost. The funding of pest management research returned to business as usual — encouraging discrete research projects with explicit short-term objectives leading to as many publications as possible. Given these constraints, it was very difficult to maintain interdisciplinary research teams working on system models. As Coulson *et al.* (1990a) stated it, "... the multidisciplinary format and centralized management approach for IPM research in forestry (and agriculture) have been virtually abandoned."

Not only did the simulation models go unfinished, but more importantly, so did the process of developing management interfaces for them. Adapting research models for farm use was a new and undefined task. Early attempts began in the mid-1980s but these were largely unsuccessful. Initial user/system interfaces were inflexible. They did not consider the manager's point of view or his way of doing business, hence they were not well accepted. The systems did not solve problems or make decisions *per se*; rather, they presented reports which had to be interpreted by the user.

Computer hardware was not ready for on-farm application of models. Most models were developed on mainframe or mini computers located at universities. These computers were the only machines that had the power to run the large models of the day. When attempts were made to distribute the models on these computers, access was difficult, costly and inconvenient for distant users. When personal computers (PC) became available in the early 1980s, they initially had limited power and prohibitive costs for individual farm use. Some models were written in computer languages that were incompatible with PC use (such as APL), and these had to be translated into FORTRAN as PCs became the machines of choice.

There was no organized method for delivering computer technology to user groups in agriculture until the late 1980s. Initially, interpreting model output was difficult and usually required research specialists. For the most part, researchers did not have the inclination to work with lay persons, and cooperative extension services were not capable of delivering this technology because of the lack of computer hardware and trained personnel. Solutions for delivering, supporting and maintaining computerize decision aids are still evolving. It is now clear, however, that resolution of these issues will require a partnership between the developers and practitioners, with an intermediary providing the link between research and application (Coulson *et al.*, 1990a). The intermediary could be an extension specialist, consultant or a technology transfer group similar to the one established for the GOSSYM/ COMAX/WHIMS system (see below). Ultimately, the resolution of these issues will determine the utility of pest management models on the farm.

There were problems with the simulation models themselves, perhaps best summarized by Gutierrez and Wilson (1989). They stated that "populations of organisms grow when birth and immigration rates are greater than death and emigration rates, and *vice versa*. The major problem in population ecology and IPM has been to define the reasons why these rates change over time and the consequences of that change on the population dynamics of pests, host plants and natural enemies. The complexity of even the simplest system has long stymied the development of 'realistic population models' for any species in nature."

The problem is not one of estimating the timing of insect life-history events. The models accomplish this task rather well. Rather, it is one of describing realistic age-specific birth, death and net immigration-emigration rates. It is extremely difficult to estimate changing abundance of populations through time and space. Take mortality for example, there are numerous biotic and abiotic factors that lead to the demise of pests; but methods for studying and quantifying their single and combined effects are not well defined. Nor do we have the ability to accurately predict future weather variables such as temperature that drive the models. These problems persist today.

INTEGRATED SYSTEMS

Stone (1989) argued that classical simulation models are inadequate as the unifying principle in IPM because they are not able to model the management process and integrate the diverse kinds of knowledge gained from the IPM projects. He believes "the process of IPM *is* management," and therefore, modeling the management process should be a major objective of IPM research. Stone (1989) called for the development of knowledge-based systems as the unifying paradigm (exemplary model) of IPM. These computer programs are designed to mimic human reasoning, the basis of decisionmaking, and can facilitate the integration of dissimilar types of information. Expert systems (ES) are the best-known examples of knowledge-based systems.

In general, expert systems have several attributes not provided by simulation models alone. These attributes include ease of incorporating management recommendations, developmental flexibility and a "user-friendly" interface for mathematical models. An "expert-in-a-box" approach is taken, capturing the knowledge of an expert (or experts) in the problem domain. A typical expert system consists of working memory, a knowledge base and an inference engine. Working memory holds the information specific for individual problems as they arise; this information is usually elicited from the user. The knowledge base is where the expertise resides, generally in the form of facts, rules (productions) and/or "frames" (Minsky, 1975). Facts are assertions about the state of the problem domain such as "the temperature is above 90F" or "there is an average of four weevils per pheromone trap." Facts provide the basic ability to represent simple, declarative knowledge.

Rules are made up of an antecedent (the "if" part) and a consequent (the "then" part). The knowledge they encode is heuristic in nature: "IF condition A exists, THEN action B should be carried out". The "action B" can represent addition (or "assertion")

of an inferred value to the knowledge base, performance of a procedure or mathematical function or advice to the user regarding the results of an evaluation.

Frames are efficient structures for storing related knowledge. Each frame consists of one or more "slots", which contain the slot name and one or more values. For example, the frame "cotton plant" might have the slots "plant height", "number of leaves" and "number of nodes" with their associated values. Most frame constructs allow a variety of items such as procedures (called methods or demons) or groups of related rules, to be put in slots. Frames allow data and associated methods to be stored together. It is thought that human beings store knowledge in conceptually similar structures, called "schemas" (Stillings *et al.*, 1987). Composite frame-and-rule-based expert systems provide powerful representational and reasoning mechanisms.

Pest management has proven to be a particularly fertile area for the application of expert systems technology. Subject areas range from rangeland grasshopper control (Kemp *et al.*, 1988) to grape pest management (Saunders *et al.*, 1987) and pesticide risk analysis (Messing *et al.*, 1989). At present, there are four expert systems for managing cotton pests in the United States. The systems are COTFLEX (Stone *et al.*, 1987; Stone and Toman, 1989), CALEX/Cotton (Plant *et al.*, 1987; Plant, 1989a), GOSSYM/COMAX/WHIMS (McKinion and Olson, 1992; Olson and Wagner, 1992), and CIC-EM (Bowden *et al.*, 1990).

COTFLEX, CALEX/Cotton and GOSSYM/COMAX/WHIMS are similar in scope, with pest management being a component of the larger farm-level system. They are designed to accommodate both simulation models and rule-bases as knowledge sources. CIC-EM, on the other hand, is a stand-alone expert system that models cotton pest management in Mississippi. It is not coupled to simulation or other management models. The details of this expert system are summarized first.

CIC-EM (Cotton Insect Consultant for Expert Management) — CIC-EM (Bowden *et al.*, 1990) is a classic rule-based expert system that deals with the management of cotton arthropod pests in Mississippi. Thirteen pests are included: thrips, cutworms, plant bugs, boll weevils, bollworms/tobacco budworms, aphids, spider mites, western flower thrips, *Frankliniella occidentalis* (Pergande), bandedwinged whiteflies, *Trialeurodes abutilonea* (Haldeman), cabbage loopers, *Trichoplusia ni* (Hübner), beet armyworms, yellowstriped armyworms, *Spodoptera ornithogalli* (Guenée) and fall armyworms, *Spodoptera frugiperda* (J.E. Smith). The knowledge contained in the program was acquired primarily from a cotton entomologist at Mississippi State University. As the result of interviews with the expert, various scenarios for pest problems were assembled, as were management recommendations for solving these problems. Because of the many possible problem scenarios, a program was written to examine the scenarios and construct a set of rules for each. This program, called the Knowledge Acquisition Program, constructs and displays the scenarios, and allows the expert to enter his recommendation. Using a pattern-matching algorithm that scans the scenarios for regularities, Knowledge Acquisition Program constructs rules that are then used in the knowledge base. Over 5,200 problem scenar-

ios were evaluated to yield 750 rules. The rules are partitioned into 13 sections along taxonomic lines.

CIC-EM evaluates a problem via question-and-answer interaction with the user. Ten to 14 questions are asked before generating a recommendation. A consultation begins with a request for the planting date and current date. The program then moves into the crop-stage identification module, where the user selects one of eight possible stages of crop phenology. After determining the crop stage, CIM-EM requests the name(s) of the pest(s) to be controlled. There are help sessions and pictures to aid in pest identification. Finally, the program invokes the rule-base partition(s) that pertains to the chosen pest(s). Using these rules, conclusions are reached which consist of recommendations and a list of pesticide application rates.

COTFLEX (COTton Farm-Level EXpert) — COTFLEX contains "advisors" in three areas of cotton production (Stone and Toman, 1989). The Farm Management Advisor and Farm Policy Advisor are small rule-bases that call and analyze the results of simulation models. The Pest Management Advisor is a more complex rule base, reflecting the nature of the pest management problem. This problem has two important features. First, pest management decisions have a strong temporal component that requires understanding of past and expected trends in crop and pest status. Second, because the agroecosystem is complex, it is impossible to enumerate all possible problem situations.

To address the temporal issue, COTFLEX stores field histories in frames. (In purely rule-based systems, the storage of related facts is inefficient for more than nominally complex situations.) From this standpoint, COTFLEX is a hybrid rule-and-frame-based system. Frames are used to store complex data and knowledge, and rules are used to perform reasoning tasks based on this information. Probably because rule-and-frame-based development environments (so-called shells) were not available at the time of initial COTFLEX development, Stone and Toman (1989) modified an existing rule-based system (CLIPS, developed at NASA) to accommodate frames. There are now many commercial shells to facilitate the development of these systems [e.g., ART-IM (Inference Corp., Los Angeles, California) and Nexpert Object (Neuron Data, Palo Alto, California)].

Model-based reasoning techniques are used in COTFLEX to deal with the inability to specify *a priori* all possible problem situations. When the system does not know the answer to a problem (i.e., when the problem is inadequately specified), it can examine a so-called "deep model" of the problem domain. This model can provide mechanistic detail about the operation of the system that is not easily embodied by "if-then rules". One form of model-based reasoning is the use of COTTAM (Jackson and Arkin 1982), a cotton simulation model. COTTAM provides COTFLEX with estimates of cotton phenology. A second variety of model-based reasoning is provided in rudimentary form via a rule base that embodies causal relationships within the agroecosystem.

CALEX (CALifornia EXpert) — This program exists in two versions: CALEX/Peaches (Plant *et al.*, 1989) and CALEX/Cotton (Plant *et al.*, 1987; Plant, 1989a,b).

More so than COTFLEX, CALEX is an "agricultural expert system shell", with inference engine, user interface, rule-language and related system components specialized for the development of management aids for agroecosystems. Thus, the knowledge in each version is specialized for a specific crop. Within each version, tasks are divided like those in COTFLEX — each has different knowledge modules and associated models. We concentrate on CALEX/Cotton, specifically the arthropod-pest component (Plant and Wilson, 1986). The system contains modules for spider mites and plant bugs.

There have been major revisions in the way CALEX makes recommendations for these two pests. These revisions illustrate the rapid changes taking place in computerized decision aids in agriculture. The original methodologies are discussed in Plant (1989a) and the innovations in Plant (1989b).

In the original version of CALEX, knowledge is stored entirely as rules (Plant, 1989a). For example, the spider mite module contains about 30 rules on in-season scouting and treatment (Plant and Wilson, 1986). The program uses a regression scheme devised by Wilson *et al.* (1985) who found that the number of infested leaves increases asymptotically over time to 100 percent. The rule base attempts to fit a nonlinear regression curve to data provided by the user. CALEX recommends in-field scouting a few days before the date of the predicted economic threshold (50 percent infested leaves). If insufficient data are available to fit the curve, simple heuristics (rules-of-thumb) are used to recommend scouting and treatment.

Plant bugs are handled with a smaller rule base that divides the season into two parts, early and mid-to-late (Plant and Wilson, 1986). Early-season treatment is recommended if the projected damage is severe enough that the crop might not have time to compensate. Mid-to-late season rules follow the University of California IPM manual for cotton (Anonymous, 1984).

Recognizing the uncertainty involved in agricultural decision making, CALEX applies certainty factors as antecedents to rules. The conclusions drawn from these rules are displayed as categories, based on the value of the derived certainty factor (c); e.g., most likely to occur ($c = 1.0$), very likely ($1.0 > c \geq 0.75$), reasonably likely ($0.75 > c \geq 0.50$) and possible ($0.50 > c \geq 0.25$). Conclusions with $c < 0.25$ are not displayed. This approach provides the user with knowledge of all reasonable conclusions.

CALEX views agricultural management as the planning and scheduling of in-season tasks, called "actions" (Plant, 1989a). For instance, a scouting trip to the field is scheduled when spider mites become a potential problem. Scouting for mites consists of walking through the field and counting the number of infested leaves in a sample (Wilson *et al.*, 1985). Obviously, field conditions can influence the ability to accomplish this task. Thus, other management actions directed at the field may come into conflict. For example, a field may be difficult or impossible to work in during or shortly after an irrigation event. Irrigation conflicts with scouting, and so does the application of pesticides and fertilizer. In the first version of CALEX, this problem is handled by a simple prioritization scheme with higher priority actions scheduled first. Irrigation has the highest priority, and so the program schedules this activity first. If the best day for scheduling a lower priority action (such as scouting) occurs when the field is wet, the action is rescheduled.

Although the original CALEX often worked well, it had three deficiencies (Plant, 1989b). First, rule bases are inherently unstructured; there are no explicit links between related items. This makes for needlessly inefficient storage and access of information that can naturally be arranged in related groups. Also, it is difficult to incorporate procedural knowledge in a rule base. Second, there are more complex interactions between actions than just time conflicts, and a simple prioritization scheme is inadequate for handling them. For example, spider mites may favor lush vegetation, prompting a recommendation to reduce irrigation in the face of high sub-threshold mite infestations. Finally, management recommendations are synthetic — they require integration of results from multiple lines of reasoning into a coherent output. The production-rule model does not efficiently deal with this type of problem.

To address these issues, basic design changes were implemented in CALEX (Plant, 1989b). Frames are now used to facilitate the storage of related knowledge in one place in the system. Frames also allow for efficient storage of, and access to, procedural knowledge in the form of methods. These procedures are stored in slots and can be accessed and activated as readily as any other piece of knowledge. For example, a mite activity frame contains data-set slots, influence-list slots (containing a list of all factors that influence an activity), and methods such as "above threshold" and "scouting date".

Farm management involves multiple objectives that are often carried out by different individuals. To deal with these problems, CALEX uses ideas from the artificial intelligence field of multi-agent planning (Konolige and Nilsson, 1980). The activities are treated as semiautonomous entities; all communication between them is accomplished through a central structure known as a blackboard. A critic module examines the blackboard and each activity to determine if there are conflicts between them before a schedule is finalized. To implement this structure, an object-oriented design was adopted. In object-oriented programming, program modules are self contained, autonomous and communicate with each other via messages. Each program unit does not need to know anything about the inner workings of the others.

GOSSYM/COMAX/WHIMS — GOSSYM/COMAX (/COtton MAnagement eXpert) represents the longest continuous research effort directed at building and applying a cotton simulation model. Experimental work began in 1964 and continues today with a collaborative insect modeling effort (Williams *et al.*, 1990). The cotton models developed during the IPM projects have their biological origin in SIMCOT II, a forerunner to GOSSYM. GOSSYM was the first cotton model to run with the assistance of an expert system, COMAX (Lemmon, 1986). While the IPM models have not been widely used by individual farmers, GOSSYM/COMAX is on many farms beltwide. The successes of this system prompted the formation of a specific group to address issues of technology transfer. The GOSSYM/COMAX Information Unit (GCIU), funded by Federal Extension Service, trains system users, promotes the transfer of the model from the research group to extension service personnel, consultants, and producers, and conveys user sentiments back to the research group for further research and development.

rbWHIMS (rule-based Holistic Insect Management System) is the pest management component of GOSSYM/COMAX/WHIMS (Olson and Wagner, 1992). It takes advantage of recent advances in software development technology, especially in the area of object-oriented programming (OOP). The idea of object-oriented programming is not new in agriculture. COTFLEX (Stone and Toman, 1989) has object-oriented elements, as does CALEX (Plant, 1989b). Sequeira *et al.* (1991) developed an object-oriented cotton model, and another is under development under the auspices of the cotton production modeling project (Sequeira and Olson, 1993). The advantages of object-oriented paradigm fall into two categories: functional and epistemological (Olson *et al.*, 1990a). The functional features are well documented (Thomas, 1989) and facilitate the maintenance and modification of complex computer systems. They are not discussed in detail here.

Epistemological (or representational) advantages stem from two facts (Olson *et al.*, 1990a). First, in a pure object-oriented paradigm system, the fundamental unit is the object. Objects consist of procedures and data. As such, the object is similar to a frame — the procedural and declarative code (i.e., the related data) are stored together as objects and accessed through a common interface. There is one critical difference, an outside procedure can directly access and modify the data in a frame. This is not the case with an object where only an object's methods can access and/or modify its data. Object orientation is intuitively pleasing because it is similar to the way we view the world — as a collection of objects, not as a collection of functions as in conventional programming techniques.

Another advantage of object-oriented paradigm, particularly with respect to modeling biotic systems, is that systems of objects can be defined hierarchically. Objects lower in the hierarchy are specializations of those at higher levels, and they "inherit" methods and sometimes data from objects above. This structure is important, because the organization of natural systems can be viewed hierarchically. The modular nature of methods, coupled with the hierarchical structure, allows detail to be represented and manipulated at multiple levels in the organization of the agroecosystem.

rbWHIMS was developed to take full advantage of the features of object-oriented programming. It contains three principal components: WhimsModel, WhimsManager and a Graphical User Interface. WhimsModel contains a static, qualitative model of the cotton/pest ecosystem (rbWHIMS does not model ecosystem dynamics explicitly, although simulation components are under development). Objects present in WhimsModel represent major components of this ecosystem. There are population objects that embody all of the pest species handled by rbWHIMS. Field, crop and management-unit objects model these aspects of the system.

As the name implies, WhimsManager manages the operations of rbWHIMS. It controls the interactions between the system and the user (through the Graphical User Interface), the accessing and operation of the rule bases and the consolidation of information and issuing of reports. Like CIC-EM, COTFLEX and CALEX, the mechanism by which rbWHIMS evaluates data and renders decisions is by the "if-then" decision rule. Unlike these systems, however, rbWHIMS is not a production-rule system.

In the production system model, the knowledge base is composed of a fact component (the fact base) and a rule component (the rule base). The fact base holds information about the specific problem being addressed, and the rule base contains the decision rules elicited from an expert. The inference engine searches the rule-base until a rule is found that matches the fact base (Waterman, 1986). When a rule is executed, one of two things happen: either a recommendation is given to the user (and the process stops), or the rule changes the information in the fact base. If the latter occurs, the inference engine searches the knowledge base again, finding the state of the fact base to be different. Therefore, a different rule will match the known facts and will, in turn, be fired. In other words, the state of the fact base determines the order in which the program executes. This characteristics gives the production system much of its power and flexibility. However, the cost in terms of program size and execution speed can be significant. An inference engine is a necessary component of the application, and repetitive searches of the knowledge base are time-consuming.

Due to the nature of cotton pest management, the developers of rbWHIMS decided that a production system approach was not needed. All the information required to make a recommendation is known in advance, as is the order in which the information is used (i.e., the order in which the rules will fire). Thus, an inference engine, *per se*, is not a part of rbWHIMS. Instead, the data needed to render a decision are collected by an object contained in WhimsManager. After manipulation, the data are passed to the rule base contained in WhimsModel, which is segmented into tree-like objects called RuleTrees. Each pest species has a set of Rule Trees. The cotton crop is divided into eight distinct, phenological plant growth stages (Williams *et al.*, 1991); and each Rule Tree is valid for one or more of these stages. RuleTrees write their recommendations to a Blackboard.

The third major component of rbWHIMS, the Graphical User Interface, provides a mouse-driven, windowing interface for the system. It is implemented in Microsoft Windows 3.1 (Microsoft Corporation, Redmond, Washington). The Graphical User Interface provides data-entry capability, menus for controlling the operation of rbWHIMS and a report-generator. The user enters field scouting information through on-screen forms displayed by the interface. These data are then used to update the state of WhimsModel. When the user requests a recommendation, a report is written that summarizes the scouting data and the recommendations provided by the system.

rbWHIMS is written in C++, an object-oriented variant of the C programming language. It currently provides management advice for the Midsouth on cutworms, boll weevils, bollworms/budworms, bandedwing whiteflies, early- and late-season plant bugs, early- and late-season thrips, spider mites, aphids, and the armyworm complex fall, beet and yellowstriped armyworms. It under- went field evaluation in 1991 and 1992, and a formal pilot test began in 1993.

The WHIMS project also has a companion sampling research effort designed to provide precise field estimates, at the least cost, for use in the model. This research is adapting innovative techniques for use in agriculture. For example, a method of scouting pest populations is under development using Bayesian statistical methods (Willers

et al., 1990). Also, an expert system component will apply Bayesian probabilities to evaluate the precision of the scouting data used in the model. This information will increase the confidence (certainty) of decisions provided by the model.

COTFLEX, CALEX and GOSSYM/COMAX/WHIMS illustrate a growing trend in the development of agricultural expert systems. Because of the complex nature of agroecosystem management, a simple rule-based format has proven inadequate. System developers are turning to advanced techniques from artificial intelligence and other branches of computer science to aid in managing large, complex bodies of knowledge. This trend is discussed below.

THE FUTURE OF MODELING COTTON PEST MANAGEMENT

The future of modeling in cotton pest management appears bright, although the models of today and tomorrow are extended in definition beyond the pure simulations of a decade ago. The on-farm successes of GOSSYM/COMAX (McKinion *et al.*, 1989) indicate that if systems are easy to use and provide a valuable service, their acceptance will be forthcoming. The organizational and synthetic abilities of computers enable large amounts of knowledge to be placed at the disposal of farm managers. Knowledge-based systems, with their ability to integrate and interpret diverse information, provide the basis for delivering powerful farm-management applications.

Jones (1989) surveyed agricultural expert systems to assess the overall viability of this technology in agriculture. He divided the existing applications into five varieties: heuristic expert systems, real-time expert systems, model-based expert systems, expert databases, and problem-specific shells. Heuristic (rule-based) expert systems are those that, in Jones' words "come close to the original concept of an expert system based on the 'seat-of-the-pants' knowledge of a tried and true expert." Although Jones (1989) predates Bowden *et al.* (1990), CIC-EM is clearly of this type. The second variety, real-time expert systems, use expert knowledge to monitor sensor data and to control instrumentation. Model-based expert systems link expert systems to simulation models to facilitate the use of the model. COTFLEX (Stone and Toman, 1989) and GOSSYM/COMAX/WHIMS (McKinion and Olson, 1992) represent this type. The fourth variety, the expert databases, link expert systems with databases to assist in the retrieval and organization of certain classes of information. Finally, problem-specific shells provide a framework within which to develop agricultural expert systems. CALEX (Plant, 1989a) falls under this category.

Jones (1989) identified heuristic (rule-of-thumb) expert systems as the least effective of the five categories for addressing agricultural management. He attributes this to the type of problem domain chosen in agriculture. When the problem is sufficiently narrow and well defined, the pure heuristic approach tends to be successful. When the domain is ill-defined and broad, the classic expert system is less viable. This attribute of rule-based systems is well known. Waterman (1986) defined a viable expert system domain as one that is narrow and well-defined. The problem domain of CIC-EM

(Bowden *et al.*, 1990) appears to be broad; there are about 750 rules for thirteen pest species. However, because the rule-base is partitioned, CIC-EM is more akin to thirteen small systems that fit the classic, narrow-domain mold. Similarly, rbWHIMS (Olson and Wagner, 1992) partitions the knowledge base (into Rule Trees) along species lines and crop stage.

Many of the tasks within agroecosystem management are too complex for the classical heuristic approach (Olson *et al.*, 1990b). Agro-management requires integration and use of advice from multiple, sometimes conflicting, experts. Further, the manager must synthesize knowledge from diverse fields. As Plant (1989b) pointed out, agroecosystem management is synthetic, and rule-bases are simply inefficient at representing such problems.

In the face of the intricate nature of agroecosystem management, builders of integrated decision-support systems in agriculture are taking advantage of developing technologies from areas of computer science, particularly artificial intelligence. As we have seen, recent systems reflect this trend in areas of object-oriented programming, causal modeling, multi-agent planning and uncertainty in decision making. In all likelihood, these trends will continue. For example, the area of causal (or qualitative) modeling (Weld and de Kleer, 1990), briefly mentioned under COTFLEX, continues to be developed in natural resource management (Schmoldt, 1991). Much of what we know about any biotic system is non-quantitative. It consists of relationships like "organism A increases as organism B decreases" or "temperature effectively limits the growth of organism C". Although these relationships are easily captured as mathematical functions, the data to parameterize these functions are often not available or, if available, are only valid for the locations and conditions under which they were collected. Olson *et al.* (1990a) maintain that qualitative relationships are often sufficient for modeling purposes, especially if the aim is not to predict actual system quantities.

Uncertainty is another area being explored in decision-support systems. Olson *et al.* (1990b) summarize the issues in natural and agricultural management, where uncertainty results from inexact measurement of system quantities or limited knowledge of system mechanisms and behavior. The Bayesian techniques under development in GOSSYM/COMAX/WHIMS address the former issue, where techniques assess the reliability of scouting information used in the model and help determine the confidence of decisions made by the model. As we have seen, CALEX/Cotton uses a certainty-factor scheme to assess the second type of uncertainty — that associated with limited knowledge. Elsewhere, Schmoldt (1991) applies fuzzy-logic techniques (Zadeh, 1965) to simulate red pine growth. Using these techniques, a causal model is developed that incorporates uncertainty in the knowledge of red pine growth and physiology. Olson *et al.* (1990c) propose another combined qualitative modeling/uncertainty technique for use in pest management systems, the Bayesian belief network (Pearl, 1988).

Spatial reasoning is another area of rapid development in decision support systems. Entomologists have long recognized that pest problems usually exhibit landscape-scale dynamics. In cotton, the only arthropod pest that is host specific in the United

States is the boll weevil. For many pests, cotton is an alternate or secondary host. These pests develop on other crops and wild hosts scattered throughout the landscape. Often they move sequentially among crops; some even migrate long distances. Therefore, the spatial and temporal scale of multiple cropping systems are important from a pest management perspective. Geographic information systems are an important tool for quantifying, modeling and manipulating this type of information.

A geographic information system is basically a database for storing spatially-registered information (Star and Estes, 1990). This information is classified by type, and stored in thematic layers. For example, a common layer contains elevation data; another layer might contain soils information, and a third might hold vegetative data. The information in each layer is spatially registered — that is, each bit of information about the layer's theme is correlated with an area that is located in some coordinate system. Each layer can be overlayed on other layers in any combination. Thus, inferences about the correlations between different values of each theme can be made. Geographic information systems usually contain sophisticated mapping features so that correlations can be visualized. They also offer, to a greater or lesser degree, software packages that allow analysis of spatial characteristics and the rectification of digital images with known coordinates.

Geographic information systems are presently being used in natural resource management, and in the past few years development has begun in support of pest management. Integrated computer systems that contain geographic components include HOPPER (Kemp *et al.*, 1988; Berry *et al.*, 1991) and the Jack Pine Budworm Decision Support System (Loh *et al.*, 1991). In HOPPER, a geographic information system helps predict the level of rangeland grasshopper infestations in conjunction with a management rule base and simulation models. The system for jack pine budworm uses a geographic information system, simulation models and a knowledge-based system to handle separate tasks. These components are linked by a database/interface that provides a common language and "look-and-feel" for all components. In cotton, a standalone geographic information system describes boll weevil populations in Mississippi (Smith *et al.*, 1993).

While the computer software developments mentioned above are moving agricultural models forward, they have been made possible by equally impressive progress in computer hardware. The rate of advancement has been astonishing, with no change in sight. Presently, PCs operate at about 100 MHz clock speeds and cost as little as $2,500. Whereas it was once thought that computer speed and cost might limit model size and application, these concerns are no longer issues of importance.

Perhaps no other research program better documents the maturation of pest management models than the Southern Pine Beetle project at Texas A&M University. This effort spans more than two decades and illustrates the continuous changes in computer hardware and software that have driven model development and application. Experimental work on beetle population dynamics began in the early 1970s as part of the IPM project. By 1980, this research led to the development of the simulation model, TAMBEETLE (Coulson *et al.*, 1989a). The first applied product, the Southern

Pine Beetle Decision Support System, SPBDSS (Rykiel *et al.*, 1984), followed in 1984. This interactive program was designed to help forest managers solve unstructured pest problems by integrating numerous models and data-bases within a single framework. It did not solve problems directly, rather only supplied managers with supplemental information for decision making. The system lacked heuristic knowledge from experts, and this shortcoming (among others) lead to the development of the Integrated Southern Pine Beetle Expert System, ISPBEX (Flamm *et al.*, 1991). ISPBEX presently contains simulation models and a treatment advisor. The advisor contains a rule base and two data bases that archive information from a national forest on beetle infestations and the red-cockaded woodpecker (an endangered species that influences beetle management). During its development, interest in beetle population dynamics shifted from single (within-spot) to multiple (among-spot) infestations. This interest led to the development of an intelligent geographic information system by the late 1980s (Coulson *et al.*, 1990b). In this system, rules are used to automate decisions based on the spatial relationships identified by the geographic component. As the integrated system enlarged, however, problems arose in connecting and maintaining the disparate components. Recognizing this, Coulson *et al.* (1989b) introduced the Knowledge System Environment, a framework that provides a protocol for connecting and interpreting diverse sources of information. Such a protocol makes it possible to add new components to extant systems.

Although we cannot predict the exact nature of agricultural models of the future, history provides important insights into their development and use. For all practical purposes, models will not be limited by computer hardware and software. In fact, the rapid technical changes in these areas are driving model development. If for no other reason than this, models will continue to increase in size and complexity, integrating new components that increase their function and ease-of-use. Today, and in the future, the factor limiting model development and use is reliable information on the dynamic biological and physical components of the agroecosystem. Reliable information is central to our ability to describe system behavior and draw sound conclusions (advice) from the models. In this sense, we have not progressed very far from the 1970s. Support of basic experimental research is essential if computerized decision aids are going to increase in function and value.

CONCLUSIONS

Sound decisionmaking in agriculture is difficult because of the complex and dynamic nature of the biotic, edaphic, climatic, economic, social and political systems involved. Decisions are often based on information that is incomplete, inaccurate, outdated or simply not available. When reliable information is available, it often describes distinct features of the production system, independent of other related factors. In formulating decisions, it is up to the farm manager to put this information into context with associated facts. Because of man's limited knowledge and experience with all aspects of the cropping system and difficulty in combining and evaluating the impact

of multiple, interacting variables on different aspects of the system, decisions are often deficient or even ill-advised. By nature, man prefers limited information on which to derive simple solutions; after all, the easy approach to problem solving is convenient, more-or-less effortless and often saves money in the short-term. Unfortunately, simple solutions rarely resolve complex problems adequately.

We demonstrate other attitudes that frustrate efforts to solve complex problems. For example, pending problems are frequently dealt with in a restrained manner, and we avoid taking action to the very last. In this sense, we are crisis-oriented. In agriculture, what constitutes a crisis with regard to pest management has been altered over the last 40 years and can be described by the general cliche, "the only good bug is a dead bug." This conviction is particularly apparent in high-value crops because of the potential losses that can result from arthropod pests. The situation demonstrates an interesting paradox. Whereas we usually are slow to address problems, this often is not the case in agriculture. Many times managers "shoot first and ask questions later" (e.g., resort to direct control when no control is needed). Just as our perception of and response to pending problems are learned, so too can our attitudes and behaviors be modified.

Clearly, individuals (and corporations) must solve problems in a cost-effective manner if they are to prosper in a competitive world marketplace. Unfortunately, experience teaches us that the quick-and-easy approach to problem solving does not always produce sound and lasting results, especially when all aspects of the production system are concerned. Consider the environment for example. What constitutes responsible problem solving from an economic and environmental standpoint is not always clear. Business considerations involving these two issues often come into conflict, with the latter losing out to the former. We are aware of this conflict more today than ever, with numerous actual or potential environmental problems in the news — industrial by-products degrading the air and water, global warming altering the climate and vegetative patterns, acid rain spoiling the lakes and forests, a diminishing ozone layer threatening public health, hazardous waste dumps littering the landscape, and a loss of topsoil degrading fertile farm lands. The fact is, there has been widespread abuse of the environment, and we can no longer be complacent of its quality. Who is responsible for its safeguard? The problem is one of scale — numerical, temporal and spatial. Individual farmers must address immediate problems (within a growing season) on a particular field(s). Within this context and to that farmer, most solutions have significant economic impact but trivial environmental impact. Unfortunately, most arthropod pest problems are regional in nature, and the management practices directed against them are usually identical. Over the years, the combined actions of all individuals in a region do have impact, and the problems arising from our ubiquitous and heavy use of agricultural chemicals constitute an excellent case in point (refer to the **Introduction** section of this Chapter).

The farmer traditionally understands man's relationship to, and dependence on, the environment. His choice of professions symbolizes this fact, which today is ironic because agriculture has become so synthetic. Man's desire to separate himself from and control nature, as opposed to integrating and working with it, is pervasive in mod-

ern society. Partly as a result, agriculture has changed from a way of life (a practiced philosophy) to a way of living (an enterprise).

In his classic monograph, Insects and Climate, Uvarov (1931) presents lasting insight into the nature of pest problems in agriculture. He states, "entomologists of the present day are no longer satisfied with merely recording the outbreaks of insect pests and with devising means for their control. They realize more and more that their chief aim and highest ambition must be to foresee and to prevent outbreaks. In order ... to do this, all conditions accompanying and causing outbreaks must be thoroughly investigated and elucidated; in other words, the epidemiology of insect pests must be the central problem of ... research, which should be carried out from the ecological point of view. The ecological conception of economic entomology consists in the recognition of the injurious insect as an integral part, and even as a product, of its environment."

One of the primary goals of entomologists is to predict pest outbreaks far enough in advance to avert disaster through proper management of pest and host (crop) populations. Surveys, or scouting, have traditionally been combined with intuitive reasoning to perform these tasks, but it is clear from the above passages that we have long dreamed of doing better. We have new opportunities to achieve this goal; however, to take advantage of them, some changes are required. The changes will not only alter our way of doing business, but our way of thinking about crop and pest management. For example, producers (and consumers) must be willing to accept some losses from agricultural pests if they are to manage populations effectively and responsibly. It is preferable to accept small losses from several pest species than significant losses from single species. This strategy does not necessarily imply greater risk.

It is unreasonable to expect producers to unilaterally alter their way of doing business without others doing the same. It is the responsibility of the entire agricultural community to provide viable, alternative management options that will ensure a competitive advantage to U.S. farmers. Computer models of crop production and management will assist in this task by providing better use of information on all aspects of the cropping system. By their very nature, these models will be complex and will require sustained, interdisciplinary efforts in their development and testing. For these reasons, modeling endeavors should not be viewed simply as research "projects", with definitive beginnings and endings. We have made this mistake before. Rather, they should be viewed as an approach to planning, conducting and transferring research knowledge. Such endeavors will provide a comprehensive and dynamic set of strategies for optimizing the costs and benefits of crop production and protection. Commitment to this approach should be widespread and lasting.

SUMMARY

This chapter charts the history of cotton pest modeling, describing the events and models leading up to the present. Examples of future systems, as we see them, are also proposed. The application of systems analysis to the study of agroecosystems, and the development of mathematical models to describe the population biologies of interacting plants and animals in these systems, has an interesting past. Cotton modeling has its origins in the 1960s and continues today with the development and application of computerized decision aids for farm management.

There have been many contributors to this fledgling science from across the Cotton Belt. Early researchers, such as the interdisciplinary teams of the "Huffaker" and "CIPM" Projects, used population models as a unifying principal of IPM. These simulation models were applied primarily as research tools, often for devising and evaluating new pest management strategies. In recent years, with the advent of economical and fast personal computers running advanced software systems, new applications have extended this technology to farm use. Simulation models are now being used in conjunction with expert systems of varying degrees of complexity. These integrated systems are designed to assist farm producers and advisory specialists in making ecologically sound decisions that optimize the costs and benefits of cotton production and protection.

Arthropod pests will continue to compete with man for food and fiber resources, and multiple tools will be needed to meet this challenge. Computers are one of these tools, and will serve an important and ever expanding role in crop management of the future. As with any new technology, however, there has been reluctance by some to embrace the modeling approach, to alter old ways of thinking and doing business. To date, their caution may be justified; the development and application of complex modeling systems have not been trouble-free. Nevertheless, the technology will prevail because useful innovations always do. The strong advocates of this approach have recognized its actual and potential value to research, education and management. Their tenacity and vision represent a challenge to all those in agriculture — to cooperate in building viable management systems that will enable U.S. farmers to maintain a competitive advantage yet be conservators of the environment.

Chapter 7

TOWARD COMPREHENSIVE ECONOMIC THRESHOLDS FOR CROP MANAGEMENT

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INTRODUCTION

Simple economic thresholds (Pedigo *et al.*, 1986; Poston *et al.*, 1983) focus primarily on the numbers of pests or their injury sufficient to cause economic loss to some commodity. These simple economic thresholds usually constitute two-dimensional verbal or graphical models consisting of pest numbers (or injury) and yields (or profits). Notable attempts have been made to add variables to the basic model (Benedict *et al.*, 1989; Brown *et al.*, 1979b; Gutierrez and Wang, 1984; Headley, 1972; Onstad, 1987; Pedigo *et al.*, 1986; Ring *et al.*, 1989, 1993; Southwood and Norton, 1973; Sterling, 1979; Sterling, 1984; Sterling *et al.*, 1992; Stern *et al.*, 1959; Stern, 1973; Wilson, 1985). The trend is to include more and more variables in the calculation of economic thresholds with the goal of developing comprehensive economic thresholds (Pedigo *et al.*, 1986), that may ultimately account for all variables influencing costs, benefits and profits of a crop management tactic.

Many factors play a role in determining comprehensive economic thresholds. Pedigo *et al.* (1986) modified the equation of Southwood and Norton (1973) to include market value of the crop, management costs, injury per insect density, host damage per unit of injury and proportionate reduction of the insect population. Onstad (1987) suggests the need for multiple and multidimensional economic injury levels for each of several control tactics if they are available. Stern (1973) showed that economic thresholds need to be qualified in terms of local climatic conditions, time of year, stage of plant development, crop involved and its purpose, plant variety, cropping practices, the desire of people, and economic variables. Unfortunately, these authors did not have a multitrophic, multipest, multifactor, dynamic computer model at their disposal with which to integrate these multiple factors, so in practice, most economic thresholds developed for use in pest management programs have been simple economic thresholds. The models of Nordh *et al.* (1988), Pedigo *et al.* (1986) and Onstad (1987), provided important new concepts for understanding the economic criteria of Stern (1973). They emphasize the importance of the multidi-

mensional needs of decision systems, however, they focus on dynamic pest injury thresholds. In contrast, control costs or benefits of control are the focus of TEXCIM for Windows. Thus, TEXCIM overcomes a major limitation (Pedigo *et al.*, 1986) of simple economic injury levels that cannot integrate multiple criteria of pests and environments.

When expanding the simple economic threshold from one focused narrowly on pests to all factors affecting the profitability of crop management, a flaw in the conceptual basis of the simple economic threshold becomes apparent. The simple economic threshold attempts to filter the flow of information through pest numbers (or pest injury) to reach a management decision (Figure 1). Because of the profit motive

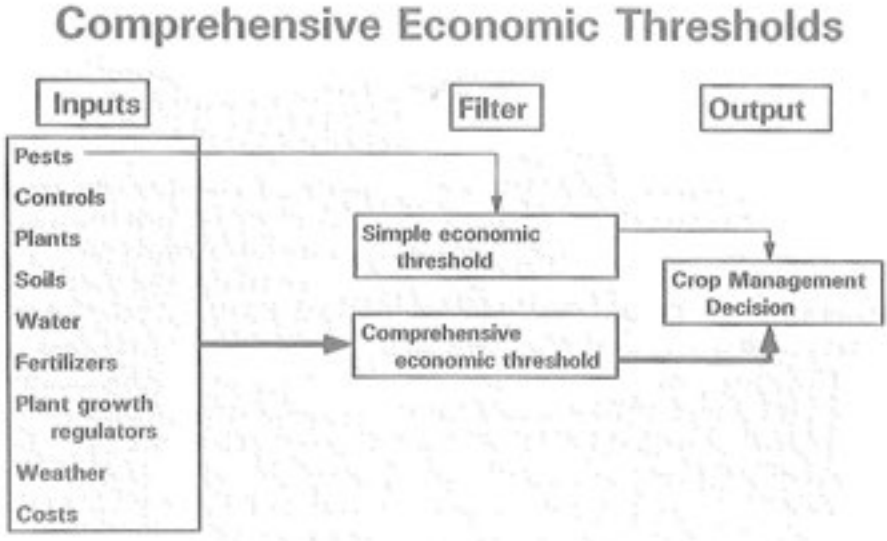

Figure 1. Filtering information inputs through a simple and comprehensive economic threshold to make dynamic crop management decisions.

of cotton crop production systems, economics provides a foundation through which all other components of the system can be filtered. Management decisions are fundamentally economic, so it makes little sense to force the flow of information through a feedback loop containing pests or injury to reach a management decision. Because of its focus on pests, the simple economic threshold has not been useful for making other crop management decisions such as irrigation, fertilization or application of plant growth regulators.

Building on the multidimensional foundation, we suggest an economically and ecologically based, dynamic, economic threshold as a further improvement of comprehensive economic thresholds for use in making tactical cotton crop management

decisions. We define the economic threshold in economic terms rather than in numbers of pests or their injury. The economic threshold is reached when the forecasted marginal costs of a management tactic equals the forecasted marginal benefits accruing from the application of a crop management tactic. This definition is consistent with that of the National Academy of Sciences (1969) for a critical pest density at which "... the loss caused by a pest equals in value the cost of available control measures," except that the focus of this definition is still on the pest. "The cost of the control measure balanced against the increased value of crop that can be recovered or protected" is the ideal way to determine when to apply a pesticide (Stern, 1973). Using multidimensional models such as TEXCIM50 (Sterling *et al.*, 1992), TEXCIM for Windows (Sterling *et al.*, 1993), TEXCOT (Unpublished data, J. A. Landivar, Texas A&M University, Corpus Christi, Texas) or ICEMM (Landivar *et al.*, 1991), it is possible to simulate the effects of many variables simultaneously, rather than focusing on a single pest density or its injury. If we assume that costs and the economic thresholds are fixed, then the comprehensive economic threshold is reached if future benefits increase to equal the economic threshold (Figure 2). In other words, profits minus losses equal zero. If benefits increase so that they exceed the costs, treatment is justified. If costs exceed benefits, treatment is not justified.

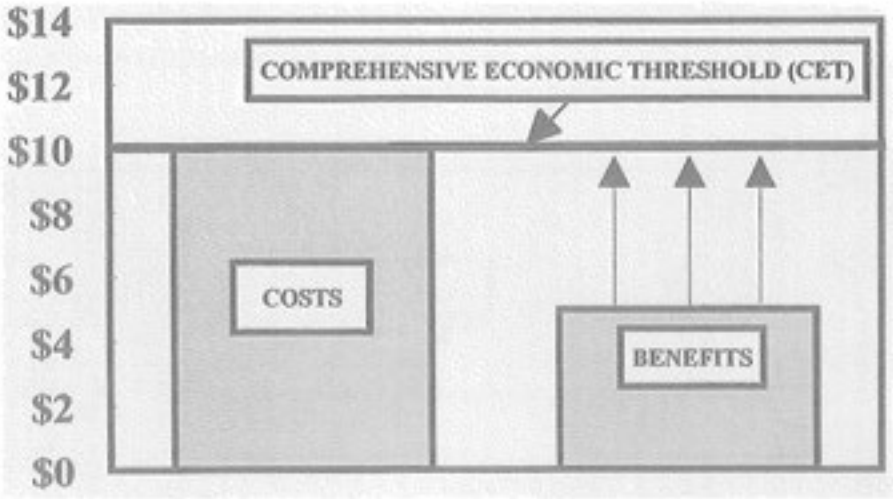

Figure 2. The comprehensive economic threshold has been reached when future benefits of a crop management tactic equal the cost of applying the tactic.

Neither costs, benefits, nor comprehensive economic thresholds are fixed; they are all dynamic. They change constantly as pests, economics, plant growth, control tactics and weather change (Figure 3). Costs, benefits, and the economic threshold may not increase or decrease simultaneously. Any one or two may increase while the others decrease. Models, such as TEXCIM, estimate these variables by making forecasts of

insect and plant dynamics and translating numbers into economics. Benefits that exceed the comprehensive economic threshold constitute the profit of control (Figure 4).

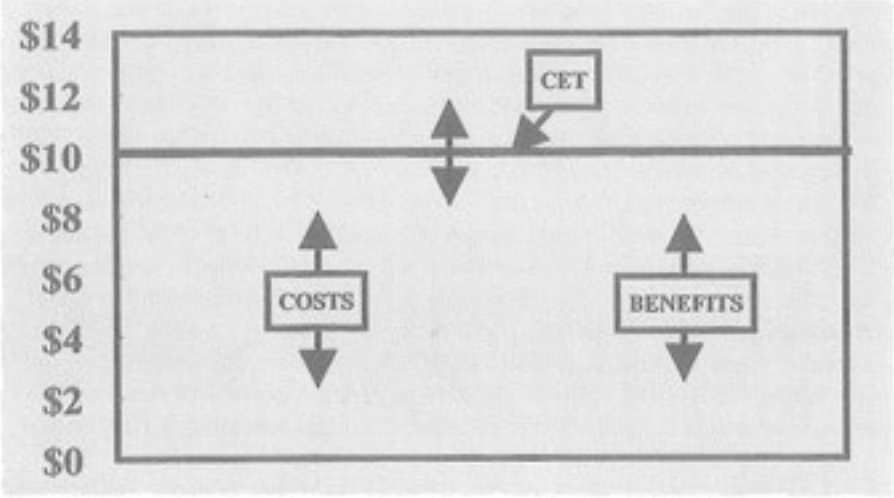

Figure 3. Costs, benefits and comprehensive economic thresholds (CET) are not fixed, they may increase or decrease independently.

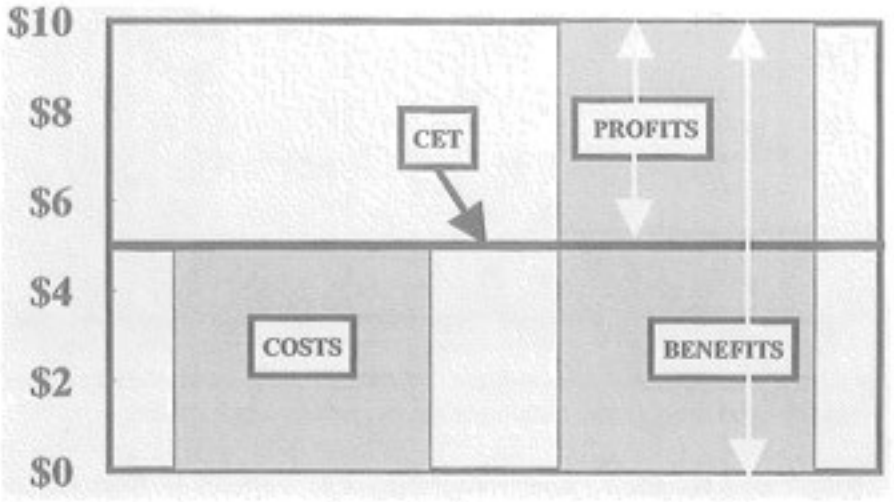

Figure 4. When benefits exceed costs, the difference is expected profit.

Computer models can now integrate many different factors simultaneously. Crop yield depends not only on pest numbers but also on any other factor that affects plant

or pest growth and development. For example, a drought-stressed cotton crop might not profit from pest control. However, two inches of slow rain on drought-stressed cotton changes the economics of pest control. Any factor, such as rain, nitrogen application, pests, predators and parasites together with any combination of soil types, crop varieties, expected price of cotton and expected yield, will change the economics of pest control, and other crop management decisions. Thus, to focus on one factor only, such as the density of pests or their injury, cannot provide reliable forecasts of the benefits of pest control. We believe that a focus on economics and pests simultaneously constitutes the best foundation for the synthesis of a modified, comprehensive, economic threshold based on economics.

In this chapter, we investigated the effect of multiple variables and their interactions on the economics of managing cotton insect pests. We also expand the comprehensive economic threshold to include other crop management decisions such as irrigation, fertilization, application of plant growth regulators and pest control.

We focus on a revised definition of economic threshold because the TEXCIM family of models help define a modified concept of the economic threshold that is dynamic and based on economics. Only by having dynamic models of the pests, their natural and introduced enemies, and the plant, is it possible to accurately estimate comprehensive economic thresholds for any particular time and place.

MANAGEMENT DECISIONS

The function of the comprehensive economic threshold is to assist in making all crop management decisions. Although most of the following discussion uses pest examples, the process should be applicable to most crop management decisions. If benefits exceed costs, the correct decision is to treat. The magnitude of the difference between costs and benefits is not critically important in making pest management decisions as long as the major costs and benefits of control are included in the calculations. If benefits are less than costs, the correct decision is not to treat. Another function of the economic threshold is to determine the magnitude of profits or losses, as depicted in Figures 4 and 5.

When costs are subtracted from benefits, the difference is profits. The profit potential of pest control may be analyzed by comparing costs and benefits of a treatment (Sterling *et al.*, 1992). For example, if the cost of control is $4.00 and the benefit is $7.00, then profit is $3.00 ($7.00 - $4.00 = $3.00). This calculation appears simple. However, these costs and benefits are composed of many sub-costs and sub-benefits (Figure 6). Control costs are <u>not</u> exclusively the costs of an insecticide and its application. Control costs include investment in consulting, insurance premiums, interest charges, costs of pest resistance that develops from the use of insecticides, resurgence of pests after insecticides kill natural enemies, health costs, and environmental costs. All costs and benefits estimated by this model are internal (single farm) only and do not include external costs to others.

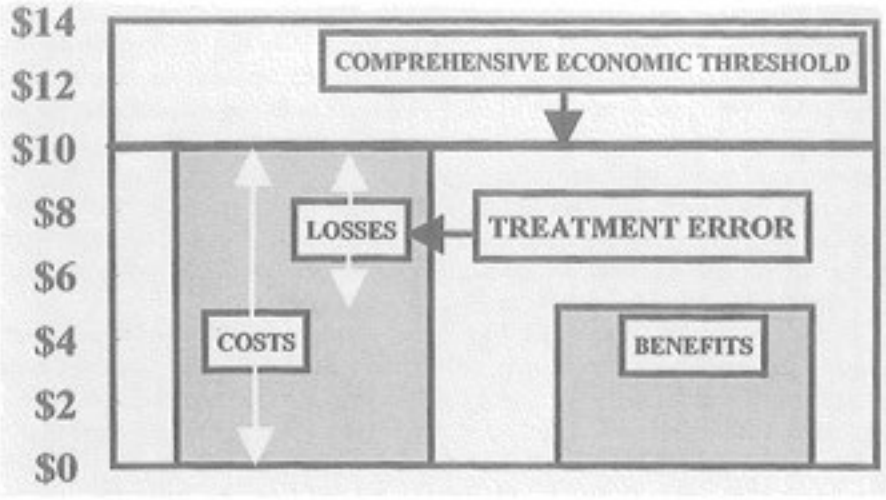

Figure 5. When costs exceed benefits of control, the difference is expected economic losses and indicate a treatment error.

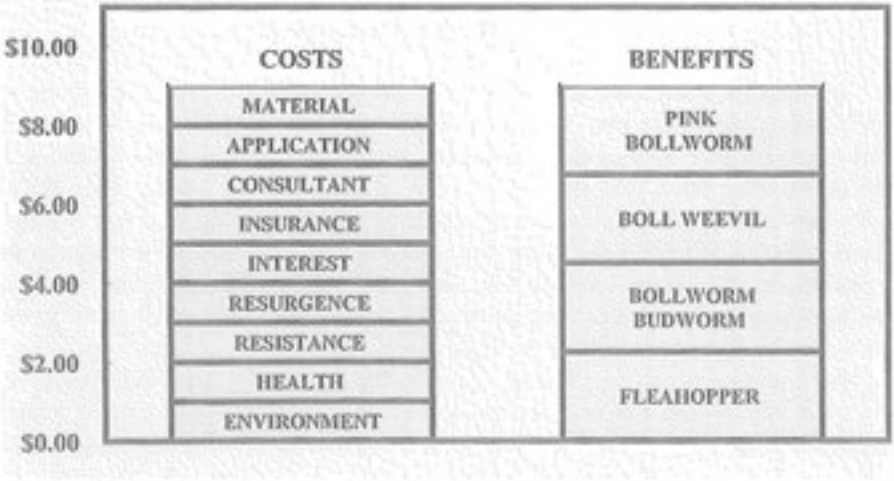

Figure 6. Allocation of costs and benefits for crop management.

COSTS

The costs of materials (usually insecticides) are often variable throughout a growing season. If an outbreak of pests expands the demand for a particular insecticide, the cost of this insecticide may increase if a shortage results. Thus, insecticides are not a fixed cost of cotton production. If pest control tactics other than synthetic

insecticides are used, such as predator or parasite releases, their costs must also be considered.

Application costs may vary throughout the season and between years. Applications by ground rig may be cheaper than by air. Ultra-low-volume applications may be cheaper than high-volume rates. Thus, application costs are not usually fixed.

Another major cost is consulting. The farmer may hire a crop consultant to assist in making crop management decisions such as those related to irrigation, fertilization, plant growth regulators, or insect, disease, and weed control. To run TEXCIM, a consultant needs to sample pests, predators, parasites, plant fruiting rate and other items. The ICEMM model requires samples of soil hydrology, soil nitrogen, soil type, organic matter, fruit for plant maps and various cultural inputs, in addition to those parameters required by TEXCIM. Weather conditions should also be monitored. Reliable sampling should lead to more profitable management decisions or the investment in sampling information is not prudent.

If an insurance policy has been purchased to cover potential litigation from the movement of an insecticide to a neighbor's property, then this cost must also be added to the cost of control. Because an insurance policy may also cover other farm-related risks of litigation, only the fraction of the policy costs that applies to pest control should be considered.

The cost of interest depends on whether the money used for pest control is borrowed from a financial institution or supplied by the grower. Investments in pest control must at least make a return equal to the interest that could be generated by other investments such as bank savings accounts, stocks, bonds, etc. The interest that could be generated with other investments constitutes a cost of control. If one borrows money from a bank for pest control, the interest paid must be added to the cost of control.

Resurgence costs constitute the difference in profit or loss when natural enemies are present, compared with the loss of natural enemies after insecticide control. If an application of an insecticide triggers an outbreak of a target or non-target pest that would not have happened without an insecticide, the difference in cost is, in part, due to resurgence.

If a higher dose of an insecticide is needed in the second application than in the first application, the difference in cost may, in part, be attributed to the cost of resistance. Or, if the same dosage of an insecticide is used with a second application but increased losses result, some of these losses may be attributable to resistance. If more frequent applications are needed to control a pest, the difference in the cost of insecticides or loss in yield constitutes part of the cost of resistance.

If the farmer, his family or farm workers are exposed to agricultural chemicals, there may be a short- or long-term health cost to the farmer, his family or employees. Often the health-related costs of insect control are delayed so they do not appear for years after chemicals are applied. This is especially true of chemicals linked to cancer, or that disrupt the endocrine and immune systems, or lower resistance to dis-

ease (Misch, 1993). Because of delayed effects, it will be difficult to know the annual health costs of chemical control. Therefore, these costs cannot be known, but can be estimated.

Using the TEXCIM for Windows model, a self-imposed (by the farmer) environmental cost is designed to address the value of not using toxic insecticides. If the pest manager has limited concern for the environment, this cost can be set to zero. Otherwise, the farmer can choose $0.25 per acre or some other amount. This self imposed cost can be interpreted as a value to the farm of not applying toxic chemicals. Those who eschew the use of toxic chemicals could claim that it would be worth $0.25 per acre not to use toxic chemicals.

All these costs are variable throughout the growing season. Some, such as health costs and insurance, can be assumed to be constant. In many cases, some costs will not be present. For example, if no insecticides are used, many costs are eliminated.

It is critically important to understand that these costs will change between fields, farms and years. Consequently, to obtain the most accurate estimate of costs, each management unit (field or farm where conditions are similar but different from other locations) will need to be considered separately.

BENEFITS

The expected crop loss can be viewed as an expected benefit accruing to the farmer if the loss is prevented with pest control. Throughout the remainder of this paper, we use the term "benefit" rather than "cost" or "loss." At first this terminology may cause confusion because pests usually do not cause benefits. Benefits are obtained only if pests are controlled; if pests are not controlled then these benefits translate into costs or losses. We choose to use the term "benefits" to be consistent with conventional usage of cost/benefits among economists. Also, there is a precedence for this choice established by Stern, 1973; Headley, 1972; and Gutierrez and Wang, 1984.

Economic benefits of control include those obtained from controlling all injurious insects simultaneously. TEXCIM currently estimates the additive benefits of cotton fleahopper, bollworm, boll weevil and pink bollworm control. If an insecticide is applied that kills some of these pests and not others, then benefits will accrue only from those killed. An insecticide that is effective against one of these insects will not result in a benefit from control of all insects. TEXCIM for Windows partitions benefits accruing to each pest controlled.

The ability to forecast the economic benefits of pest control is one of the most powerful features of this model (Figure 7). By comparing the losses in a treated cotton field compared to an untreated one, the benefits of controlling all pests can be estimated. Forecasts are accomplished by using a multitude of factors that affect the reproduction, growth and death of each insect and cotton fruiting structures. The time required for an insect to complete development, or a fruit to mature, depends largely on temperature. Organisms generally grow faster and reproduce more rapidly in hot than cold conditions. They lay more eggs when their food quality is high, and

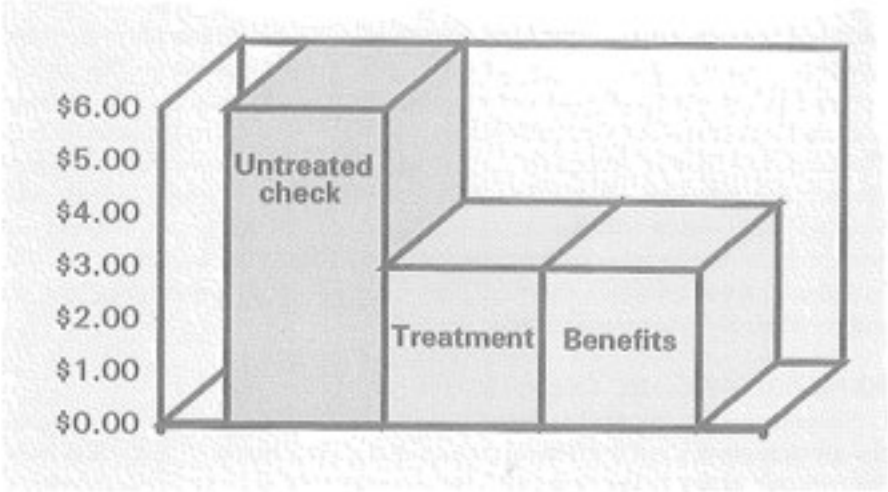

Figure 7. Forecasted benefits calculated as the difference between losses in an untreated check and a treated plot.

more die when their natural enemies are abundant. Temperature, rain, food quality and natural enemies are only a few of the many variables that operate within the model to make forecasts. It is virtually impossible for the human mind to simultaneously take all these factors into consideration in making management decisions. Computers are uniquely qualified to make these simultaneous calculations and forecasts.

MARGINAL COSTS, BENEFITS AND PROFITS

All the costs, benefits and profits mentioned are "marginal" in the sense that they are the consequences of making a future treatment and do not represent the cumulative consequences of multiple treatments in the past. For example, if two treatments have been made and we wish to estimate the economic consequences of an additional treatment, this third treatment is the "marginal" treatment. "Marginal" is a term with a long history of use in economics, which we have adopted to help explain the application of economics to pest management decisions.

ECONOMIC THRESHOLDS AND CURRENT MANAGEMENT

The economic threshold has been the cornerstone of integrated pest management (National Academy of Sciences, 1969). Unfortunately, reliable economic thresholds still exist more in theory than in practice. Some criticisms of economic thresholds are that they seldom: (a) consider the simultaneous interactions of multiple pests, (b) integrate the impact of multiple natural enemies of the pests, (c) are dynamic concerning plant development, or (d) change with expected lint prices. Consequently,

economic thresholds in current use and those that have been proposed should be used with caution. On the other hand, the use of economic thresholds in pest management programs have shown potential in spite of their weaknesses. Six on-farm cotton IPM trials using economic thresholds reduced insect control costs, increased yield in 50 percent of the cases and reduced costs in 66 percent of the cases in Texas (Lacewell and Masud, 1985). The same trend exists in other agricultural systems (Frisbie and Adkisson, 1985). Thus, the economic thresholds used in these trials were an improvement over the exclusive reliance on calendar day insecticidal control and have functioned as useful "rules of thumb." However, as with any working hypothesis, these economic thresholds are subject to replacement when new and improved methods become available.

NEED FOR DYNAMIC CRITERIA

Simple economic thresholds have often been expressed as a constant throughout the growing season or for extended periods during the growing season. Because of the dynamic nature of the crop and insect numbers, dynamic economic thresholds have been recommended. Brown *et al.* (1979a) developed dynamic economic thresholds for bollworm, Curry and Feldman (1987) for boll weevil, and Gutierrez *et al.* (1979) for western lygus bug, *Lygus hesperus* Knight. These authors concluded that there is a need to replace static management criteria with dynamic ones but models capable of dynamically calculating these criteria have not generally been available or sufficiently user-friendly for use by crop managers or researchers. These authors apparently accept the notion that a dynamic economic threshold can be based on insect numbers or injury. We believe that replacing the economic threshold based on pest numbers or injury with comprehensive economic thresholds provides an analytical method for avoiding the limitations of the simple economic thresholds and will ultimately result in improved pest management decisions.

MULTIDIMENSIONAL ANALYSIS

Several models have been used to evaluate the impact of multidimensions on the economics of cotton production (Nordh *et al.*, 1988). Various control tactics such as pesticide timing, host plant resistance and natural predation and parasitism were analyzed by Curry *et al.* (1980) using an earlier version of the boll weevil model now incorporated into TEXCIM for Windows. They observed that relatively small reductions in the growth rates of boll weevil populations may provide economic control of this pest. Brown *et al.* (1979b) also evaluated the interactions of the cotton crop and insect pests. Gutierrez *et al.* (1975) investigated the interactions of plant age and beet armyworm, *Spodoptera exigua* (Hübner), injury and observed that the greatest injury primarily occurred during the early squaring period. Similar multiple-component studies have been conducted by Stinner *et al.* (1974a) and Wilson *et al.* (1982). Thus, there is a growing body of literature dealing with the importance of multicomponent models for improving the science of pest management.

MODEL VALIDATIONS

The TEXCIM model was first released for popular use by the Texas Agricultural Experiment Station and was made available through the Texas Agricultural Extension Service in 1988 with version 2.3 (Hartstack and Sterling, 1988b). It was followed by version 3.0 (Hartstack and Sterling, 1989), version 4.0 (Hartstack *et al.*, 1990), version 4.1 (Hartstack *et al.*, 1991), version 5.0 (Sterling *et al.*, 1992) and TEXCIM for Windows (Sterling *et al.*, 1993). These versions constitute multipest, multitrophic, multicomponent computer models. They increase in complexity until the latest versions use field counts of cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter), bollworm, *Helicoverpa zea* (Boddie), tobacco budworm, *Heliothis virescens* (F.), boll weevil, *Anthonomus grandis grandis* Boheman, pink bollworm, *Pectinophora gossypiella* (Saunders), 10 groups of predators, 10 groups of parasites, insecticides, cotton fruit, and local weather to forecast the expected benefits of control. The user's guides are accompanied by protocol for testing the model (Sterling *et al.*, 1989b, 1990b). Other specific methods used in the following simulations are provided as part of the results reported in this paper. An unpublished version currently under development includes ICEMM (Unpublished data, J. A. Landivar, Texas A&M University, Corpus Christi, Texas). In addition to the insects included in TEXCIM, ICEMM includes separate models for the tobacco budworm, the cotton aphid (*Aphis gossypii* Glover) and the sweetpotato whitefly (*Bemesia tabaci* Gennadius).

One important feature of models such as TEXCIM and ICEMM is that they provide a testable and falsifiable hypothesis. Often, models and their code remain in the tight control of their developers so that testing by other parties is very difficult. Versions of TEXCIM and its components have been tested in 26 separate experiments conducted by many different groups of scientists (Sterling *et al.*, 1993). This validation process has consisted of repeated development, testing, revision and retesting as an iterative process that is the essence of the scientific method. These validations lend credence to the value of using the TEXCIM model for the simulations presented in this paper, in commercial pest management, and as a basis for improving future models of this kind.

METHODS FOR ESTABLISHING COMPREHENSIVE ECONOMIC THRESHOLDS

Field experiments can be conducted that will explain the simultaneous effect of several pests (National Academy of Sciences, 1969). But, when all the permutations and combinations of pests (insects, weeds, diseases and nematodes), pest age, plant stage, fruit age, plant cultivar and weather are considered, it becomes virtually impossible to conduct such a field test that will incorporate all these components with each one varying in replicated, multifactorial experiments. The standard method used to determine simple economic thresholds is to use replicated field or

caged plots so that a single variable, such as pest density, changes in each treatment while all other variables are held constant. Yields at the end of the year are then used as an index of the impact of different variables such as pest densities. "Because costs involved with developing economic thresholds can be substantial, a resultant effect is that experiments often have either insufficient replication or insufficient damage levels for deriving accurate economic thresholds. An alternative to conducting detailed field threshold trials is to use a crop-pest simulation model with simpler field trials" (Wilson, 1985).

Furthermore, field plot experiments to determine multiple pest effects are very complex. The permutations and combinations of variables in such studies make it unlikely that more than about three or four treatments can be changed in any single experiment. For example, the combinations of just three treatments with four replications each requires 24 plots and four treatments would require 96 plots. Coupled with the general inability to eliminate all variables but one in field plots, an accurate determination of the effect of each variable is unlikely. Also, because of multiple pest interactions the effect of several pests is not simply additive. The benefits of insecticidal control targeted against a specific pest can seldom be attributed to the control of that pest alone when several pests are present simultaneously. Thus, there is a need for multiple-pest decision criteria that are sensitive to plant growth stage and future insect and plant fruiting dynamics. Computer models can handle all these variables and make sense of multiple interactions of herbivores and fruit dynamics. These models can then be tested under commercial and experimental conditions and various components improved as evidence shows the need for such improvement (Breene *et al.*, 1989; Legaspi *et al.*, 1989; Sterling *et al.*, 1989b).

The problems of using field experiments to establish decision criteria are clear from work on *Helicoverpa/Heliothis* spp. conducted around the world. Different authors have found different criteria suitable for their conditions (Adkisson *et al.*, 1964; van den Bosch *et al.*, 1971; Wilson *et al.*, 1982). This evidence supports our hypothesis that benefit/cost ratios will not and cannot be precisely the same in different times and places. The most important observations from the simulations run in this paper is that no single factor such as pest density, lint value or time can be used alone to forecast benefits of control. All these factors must be considered simultaneously.

REDEFINING THE ECONOMIC THRESHOLD

"Economic thresholds can vary with stage of crop development, are modified by whether damage has occurred earlier in the season, vary depending upon the relative abundance of predators, and are affected by season length. They are dynamically associated with the market value of the crop and with management costs" (Wilson, 1985). The definitions of an economic threshold that focus primarily on pest density (Headley, 1972; Stern, 1973; Stern *et al.*, 1959) or pest injury (Onstad, 1987; Pedigo *et al.*, 1986) are approaching obsolescence and a new definition is in order. This is especially true if Pearson (1958) is correct when he asserts that neither pest numbers

or their injury are valid indications of yield or quality of lint. A new definition must integrate not only pest numbers or their injury but their economic impact in association with other key factors that affect the economics of pest management decisions. Although all factors affecting the economics of decisions are not currently available in any model, sufficient factors are present in the TEXCIM model (Sterling *et al.*, 1993) to augment the new economic threshold concept.

Another major problem with economic thresholds currently in use is that multiple key variables have not been integrated into their calculations. Thus, the preliminary economic thresholds that were developed and used in pest management programs were simplistic and could not always be accurate in all places. Although it was obvious long ago that the economic threshold would be a function of local climate, time of year, stage of plant development, plant variety, cropping practices and economic variables, the methods and tools for calculating or forecasting such a level were not available (Smith, 1971). A comprehensive economic threshold concept has been slowly evolving so that factors such as control costs, crop phenology and multiple species are now sometimes considered in making management decisions. Southwood and Norton (1973) determined that economic damage was a function of yield, price per unit of yield, level of pest injury and control actions. These additions were only a beginning compared with the complexity needed to make consistently accurate pest management decisions.

TEXCIM provides information useful in making management decisions concerning the need for insect control. Field tests of an earlier version, TEXCIM30, showed that correct decisions were made greater than 95 percent of the time (Legaspi *et al.*, 1989) compared to simple economic thresholds. Whether the error is on the side of taking action when none is needed (treatment error) or taking no action when a need exists (no-treatment errors), dynamic models such as TEXCIM for Windows should prove useful.

Some of the first order components of the TEXCIM50 model are presented in mnemonic form (see Sterling *et al.*, 1989a for more details) where f is a function:

MGDC = management decisions
MGDC = f(BC,CET)

1.0 BC = benefits of pest control (forecasted cost of pest injury)
BC = f(CVA,IIJ,CS)

1.1 CVA = value of crop (see Sterling *et al.*, 1989a for multiple subcomponents)

1.2 IIJ = injury by insects
IIJ = f(HIJ,BIJ,WIJ,PIJ)

1.21 HIJ = fleahopper injured fruit
HIJ = f(HNU,HAG,CAG,HFP,HSF,HPF)

1.211 HNU = numbers of fleahopper (includes 37 sub-components)

1.212 HAG = fleahopper age

1.213 CAG = crop age

1.214 HFP = fruit age preference of the fleahopper
1.215 HSF = number of susceptible fruit
1.216 HPF = probability of fleahopper finding a fruit
1.22 BIJ = bollworm-tobacco budworm injured fruit (See Sterling *et al.*, 1989a for multiple sub-components)
1.23 WIJ = boll weevil injury (See Sterling *et al.*, 1989a for multiple sub-components)
1.24 PIJ = pink bollworm injury (sub-components about same as for fleahopper).
1.3 CS = costs of pests surviving control
2.0 CET = comprehensive economic threshold
CET = f(INCO,IRS,IRE,INPO,ISCO,HECO,APCO)
2.1 INCO = insecticide cost
2.2 IRS = resurgence of insects
2.3 IRE = increased insecticide resistance
2.4 INPO = environmental pollution with insecticides
2.5 ISCO = insurance cost
2.6 HECO = health cost
2.7 APCO = application costs
APCO = f(LACO,EQCO)
2.71 LACO = cost of labor
2.72 EQCO = cost of equipment

Most of the components of the TEXCIM for Windows model can be found in a synthesis of TEXCIM40 (Sterling *et al.*, 1989a). This synthesis provides an abbreviated verbal description of the various components that play a role in forecasting benefits of pest control and references documenting mathematics and functions.

TEXCIM SIMULATIONS

The methods used here are a form of sensitivity analysis where a parameter or state variable is changed over a reasonable range to simulate expected benefits of controlling a particular pest or group of pests. A complete set of data on insect pests, predators, fruit, and weather is available from experiments conducted at Snook, Texas during 1989. These data, or parts of the set, were used for many of these sensitivity analyses. To determine the benefits of pest control, simulations were run using the TEXCIM50 model (Sterling *et al.*, 1992).

The following simulations are not designed to provide fixed benefits of value at any particular time or place, but to demonstrate the variability of control benefits that are conditional upon multiple factors. In order to determine these benefits for any particular time and place, it is necessary to enter current information on insect pests, predators, fruit counts and weather into the TEXCIM50 or TEXCIM for

Windows model and run it. An example of a complete data set used in these simulations is provided as example files provided with a copy of TEXCIM for Windows.

JUSTIFYING A CONTINUUM

The Texas Agricultural Extension Service cotton insect control guide (Knutson *et al.*, 1993) provides simple economic thresholds of the cotton fleahopper that vary from 10 to 15 fleahoppers per 100 plant terminals during the first three weeks of squaring. At the appearance of first bloom the threshold increases to infinity and the crop supposedly can tolerate any number of fleahoppers. There are two elements of these thresholds of interest: (a) they are dynamic in the sense that they change at least once during the growing season and (b) a range of thresholds (10 to 15 percent) is provided as an option for the pest manager. Testing with the TEXCIM40 model (Hartstack *et al.*, 1990) indicated that neither the 10 percent or 15 percent threshold was likely to be accurate for all cotton production systems. For example, the economic threshold is unlikely to change from 15 percent to 100 percent in one day (date of first bloom). This change is more likely a continuum of the type shown in Figure 8. Benefits change continuously over time, not in two discrete steps. Under

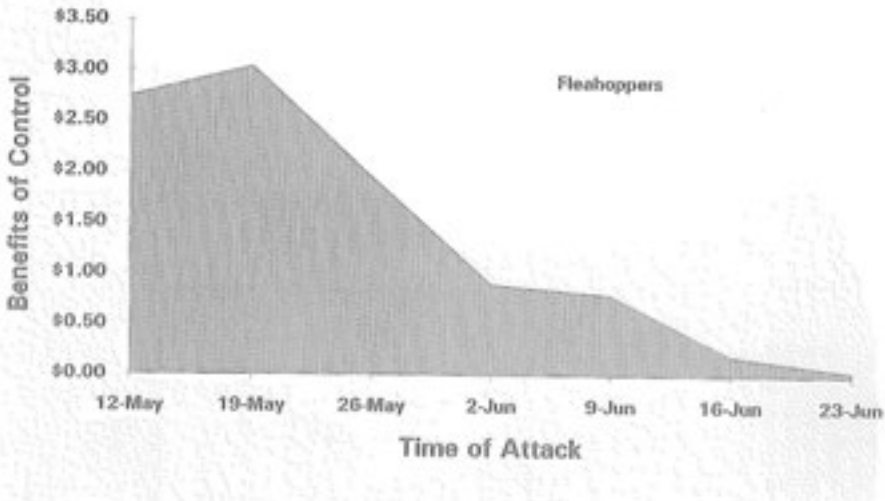

Figure 8. Benefits of cotton fleahopper control as a function of the time of attack during the growing season.

the scenario used in this example, the time of fleahopper attack was simulated on May 12 when a total of 15 fleahoppers per 100 plants were entered to mimic the lower economic threshold. The time of injury was then changed with all 15 fleahoppers entered on May 13, then on May 19 and so on until at last 15 fleahoppers

were entered only on June 30. The same number of fleahoppers were entered at weekly intervals from the time of first square until after first bloom. The benefits of controlling these fleahoppers were highest at the time of first square and declined until about the time of first bloom. Thus, the decline in benefits of fleahopper control forms a continuum of costs from a high of over $3.00 per acre to $0.00 on June 23. The magnitude of benefits will vary in other cotton fields in other years, but changes should form a continuum similar to Figure 8. In other words, the benefits of controlling 15 fleahoppers per 100 plants changes continuously as a function of the time of attack on the cotton plant.

FACTORS DETERMINING THRESHOLD VALUES

Time of Insect Pest Attack — Onstad (1987), Ring *et al.* (1993) and Wilson (1985) emphasized the importance of including time in relation to numbers of pests changing over time. TEXCIM50 was used to test the hypothesis that time is important as it relates to other factors. Field counts of bollworm eggs and small larvae formed a pulse (a single peak) that lasted about one month during 1989 at Snook, Texas. This pulse, represented by peak abundance of 1.4 eggs and 0.3 larvae per 3.1 feet (1 meter of row) was entered into TEXCIM50 and run at 2-week intervals starting at the time of first square to simulate the change of control benefits as a function of time of attack. Data on other pests and insecticides were not included with this run of the model. All variables were held constant except time of attack. The price of lint was set at $0.62 per pound and the target yield at 1.2 bales per acre (dryland).

Under the above scenario, the benefits of controlling a single pulse of bollworms changed dramatically from $20.00 per acre to about $4.00 per acre, at different developmental stages of the cotton crop (Figure 9).

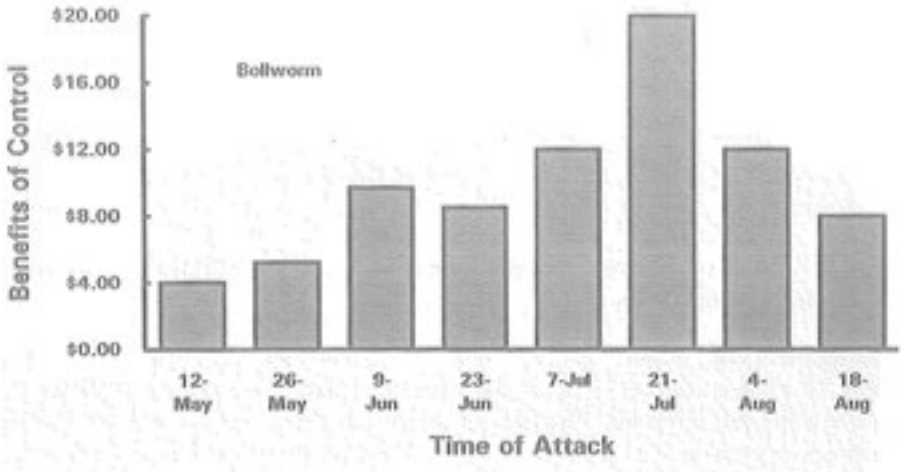

Figure 9. Forecasting the benefits of bollworm control when the time of attack varies during the growing season.

In general, developmental stage of the plant is an important factor in determining the benefits of bollworm control. It is clear from this simulation, that basing a decision on the presence of any pest would be inaccurate if the same criterion were entered at different stages of plant growth. Under other scenarios, including other insects or insecticide use, the pattern of benefits attributable to bollworm control would be different. However, based on this simulation it is reasonably certain that benefits of bollworm control will be, in part, a changing function of the time of bollworm attack. Only a dynamic crop-insect-predator model could begin to integrate changes over time in such a dynamic fashion to forecast benefits of control.

Geographical Variation: Bollworm — Historical weather data from Lubbock, College Station and Weslaco, Texas were entered with the same bollworm pulse (same as the "time" simulation used above) to simulate the impact of weather at three locations on benefits of bollworm control. The same numbers of bollworm were entered for each geographical area and other factors were held constant. This simulation forecasts the benefits of bollworm control at three locations that exhibit different weather patterns. In general, location and its associated weather did not have a major impact in that benefits of bollworm control varied little among areas. In other words, TEXCIM50 was not very sensitive to weather differences at the three geographical locations under the conditions of this simulation. The greatest difference was only $1.65 between Weslaco and Lubbock with essentially no difference between Weslaco and College Station (Figure 10). In any given year, the economics of pest control between geographical areas is likely to be sufficiently different so that forecasts in one area are unlikely to be accurate in another, even with the same number of pests. This conclusion speaks to the importance of making independent pest management decisions for each field or management unit.

Geographical Variation: Boll Weevil — Studies designed to identify factors causing mortality of boll weevil in Texas produced a clear pattern of the impact of mortality resulting from heat and drying (Sterling *et al.*, 1990b; Sturm *et al.*, 1990; Sturm and Sterling, 1990). Average drying-caused mortality increased westward from the eastcoastal region to the midwestern region. Drying-induced mortality averaged 9 percent in the eastcoastal region, 30 percent in the northcentral region and 57 percent in the midwestern region of Texas. Benefits to the farmer from boll weevil mortality from drying can be calculated using the TEXCIM model. The greatest benefits of death caused by drying should occur in western regions of Texas. Benefits of boll weevil control at Snook, Texas were compared to benefits at Pecos, Texas. Snook characteristically enjoys high rainfall whereas Pecos is substantially dryer and hotter during the growing season. Therefore, it is intuitive to expect more boll weevil mortality caused by drying at Pecos than at Snook. Historical weather data were entered for each location, no predators were entered, and 15 percent weevil injured squares were entered three weeks after the first square. The benefits of boll weevil control was $70.37 more at Snook than in Pecos (Figure 11). This may be interpreted as a $70.37 potential benefit that farmers at Pecos enjoy because of

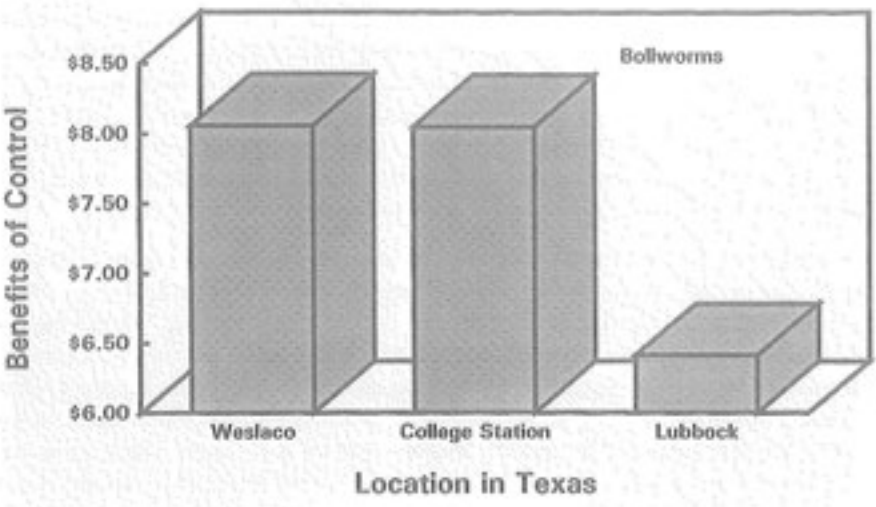

Figure 10. Simulated benefits of controlling identical numbers of bollworms at first bloom at three locations in Texas.

heat and drying if insecticides are not used. Of course this benefit may be offset by other costs of cotton grown in a dry climate.

Lint Value — The quality of lint affects its value and anything that affects the value of lint will change the economic threshold. If control measures are not undertaken at the appropriate time, there may be increased costs for washing, brushing, trimming, sorting or grading the crop at harvest. The value of fruit is a function primarily of time of the growing season and age of fruit (Hartstack and Sterling, 1988a; Stewart, 1987; Stewart and Sterling, 1987). As fruit mature they become more valuable because they are less likely to shed due to minor stresses. Thus, an open boll is more valuable than a square, bloom or green boll.

Field data for bollworm, predators and weather for Snook, Texas were again entered into TEXCIM50. Lint value alone was changed with each run. The benefits of bollworm control is a linear function of lint value (Figure 12). If lint was valued at $0.50 per pound, the pulse (peak) of bollworms realized a control benefit of only about $17.00 per acre. When the value of lint increased to $1.00 per pound, the benefits of bollworm control increased to about $33.00 per acre. Thus, decision criteria are dependent on lint value.

Planting Date — Simulations of the benefits of bollworm control were based on changes in planting date at 5-day intervals starting April 8 and ending June 3. All other factors including bollworm numbers and harvest date were held constant and based on field count data for the Snook, Texas untreated field during 1989. Numbers

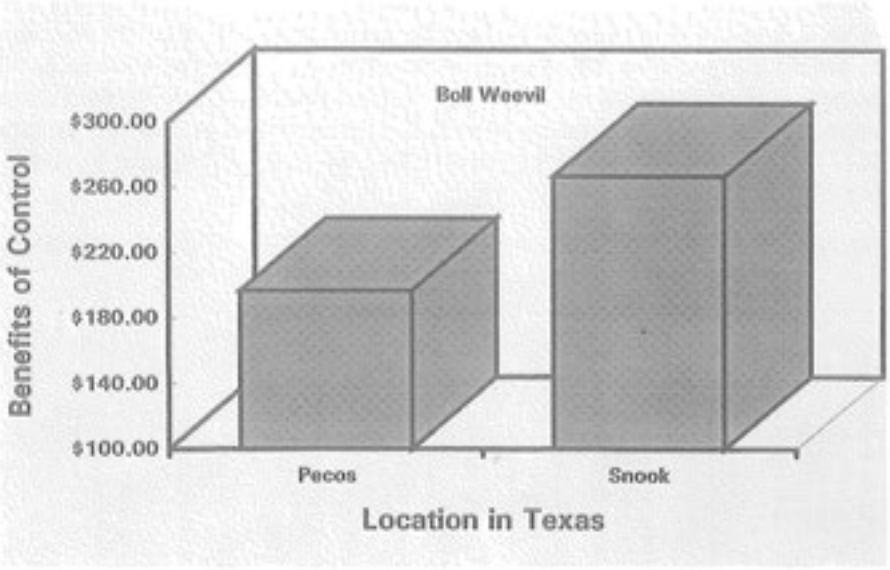

Figure 11. Geographical variation in benefits of boll weevil mortality caused by drying in Texas.

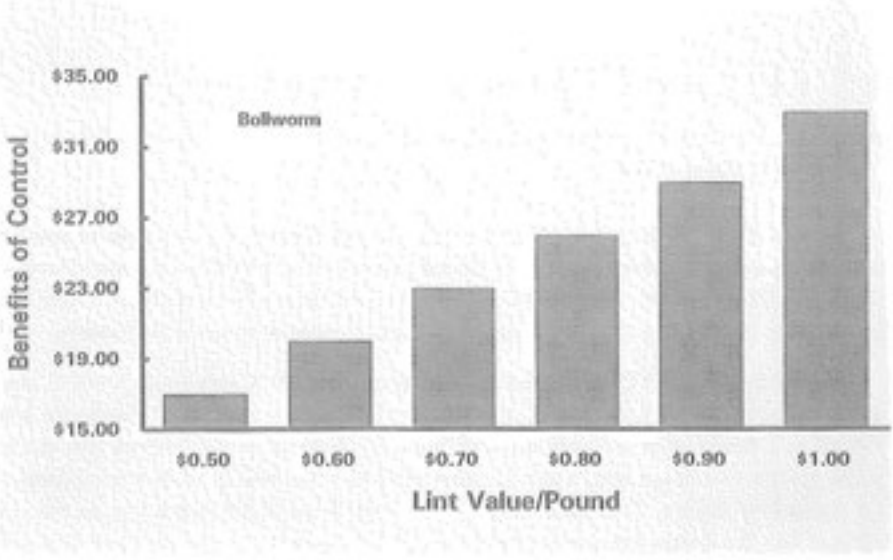

Figure 12. Benefits of controlling constant numbers of bollworms as a function of lint value.

of naturally occurring predators were included. Benefits of bollworm control were partly a function of planting date. Benefits varied little until May 20 then they declined rapidly (Figure 13). Data presented here should not be used to justify changes in planting date in any particular area since planting date will have a different impact on yield and crop value, in part as a function of area or geographical location. TEXCIM must be run using current data from each geographical location to provide reliable forecasts.

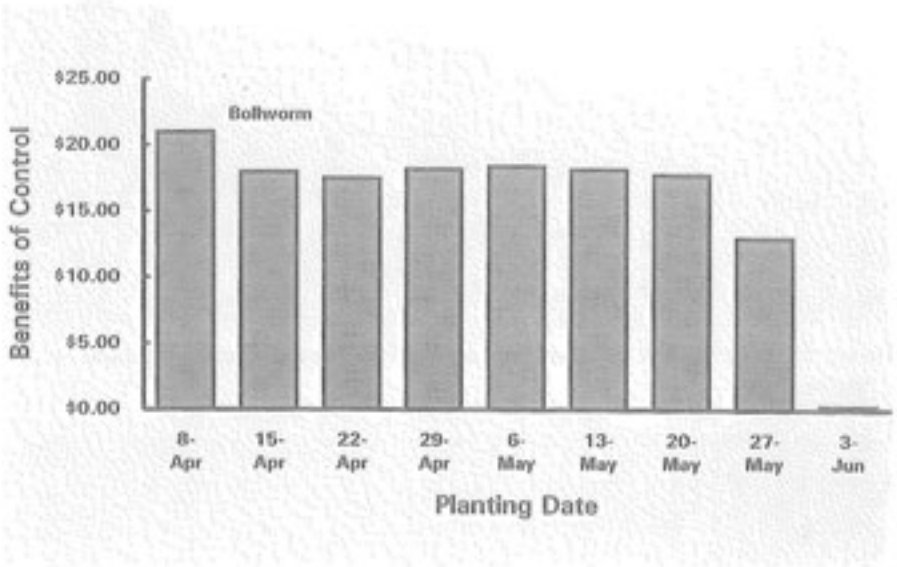

Figure 13. Benefits of controlling constant numbers of bollworms as a function of changes in planting date.

Harvest Date — Benefits of controlling the bollworm is a function of harvest date. With the particular scenario of Snook, Texas data, benefits of control were a function of harvest date (Figure 14). A later harvest date allows bollworm numbers to continue developing late in the growing season, causing greater boll injury.

Row Width — TEXCIM contains a boll weevil model (Curry *et al.*, 1982; Curry and Feldman, 1987; Schoolfield, 1983) that simulates mortality of immature boll weevil as a function of temperature and humidity. One of the features of this model is the ability to change row width to determine its relationship with weevil mortality caused by drying. The wider the rows, the more sunlight penetrates to the soil surface and the hotter the surface becomes. Weevils on hot soils die from heat and drying. The TEXCIM50 model was used to simulate the impact of 10- to 50-inch row widths, changed at 10 inch increments and holding all other factors constant. Temperatures entered were from historical average temperatures from Pecos, Texas.

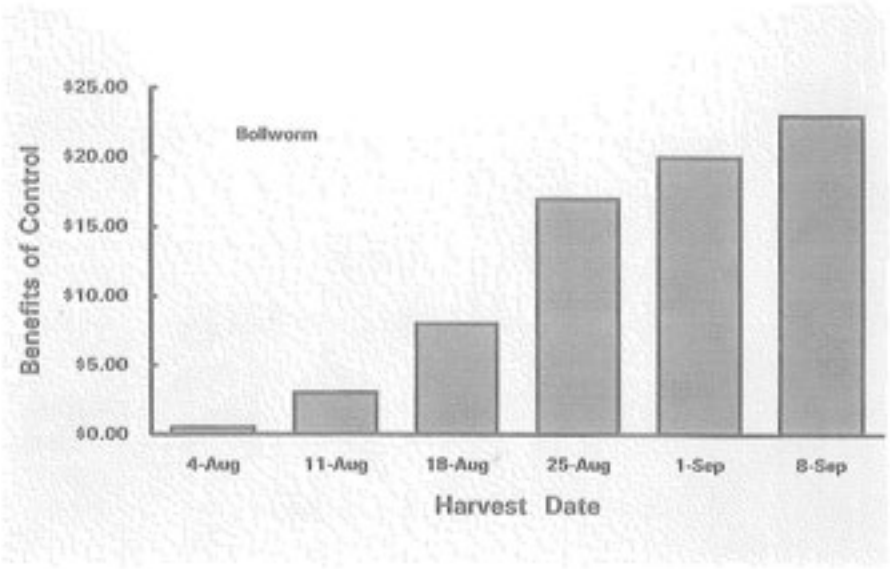

Figure 14. Benefits of controlling constant numbers of bollworms as a function of harvest date.

This location was chosen because some of the highest temperatures and lowest humidities in Texas occur at Pecos.

As row width changed from 10 to 50 inches, the benefits of boll weevil control decreased from $35.20 to $27.78 per acre (Figure 15). Thus, the potential benefit of increasing row width may be as much as $7.42 per acre if boll weevil are abundant and in hot-dry climates. In areas where boll weevil are a problem in Central and West Texas, there may be some value in making a change in row width to take advantage of boll weevil mortality caused by drying.

Row Orientation — Row orientation may at times be important in relation to boll weevil mortality caused by drying. Drying is more important as a mortality agent of boll weevil in hotter, drier parts of Texas (Sturm and Sterling, 1990; Sturm *et al.*, 1990), so Pecos, Texas was chosen. Historical weather data from Pecos was entered but all rainfall was removed to insure maximum drying mortality. A short-season (160-day) cotton variety, no insecticides, and 15 percent damaged squares were entered two weeks after the appearance of the first square. Two row orientations, north-south (0 degrees) and east-west (90 degrees), were entered.

Benefits of boll weevil control were $1.09 more per acre when rows were planted in an east-west direction than in a north-south direction. Thus, in dryland cotton production areas of West Texas, orienting the row direction so that sunlight falls on the soil surface between the rows enhances weevil mortality. This row direction results

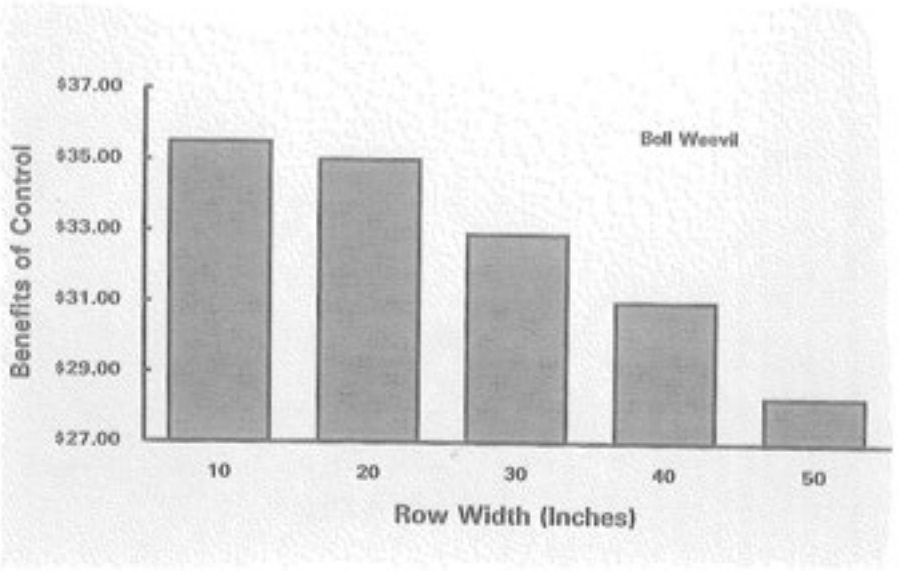

Figure 15. Benefits of boll weevil control as a function of row width.

in greater exposure of immature boll weevil in squares on the soil surface to the drying of solar radiation than if rows ran north-south. As temperature (Sterling *et al.*, 1990a) and solar radiation increase, boll weevil mortality also increases. However, TEXCIM50 was not very sensitive to row orientation as indicated by the low benefit of only $1.09 per acre.

Target Yield — Cotton fleahopper numbers were held constant (Snook, Texas 1989 data) and target yield was changed with each run of TEXCIM50. The target yield in TEXCIM50 functions to set limits on potential cotton yields per acre. With all other factors held constant, the benefits of controlling fleahopper increased from about $17.00 per acre at a target yield of 0.5 bales per acre to about $41.00 per acre when the target yield was increased to 1.5 bales per acre (Figure 16). If we expect a yield of 1.5 bales per acre, there is very little room for plant compensation of fleahopper injury. With lower expected yield, compensation is more likely. Apparently, plant compensation for fleahopper injury explains the difference in benefits.

Plant Variety — Different cotton varieties can be chosen in TEXCIM50 by changing the growth rate of the plant. Short-season varieties (<140 days) grow rapidly compared to very long-season varieties (>200 days). The user can change these values to calibrate the cotton model in TEXCIM50 to his own crop. The benefits of controlling fleahoppers is dependent on the variety of cotton grown (Figure 17). Under the conditions at Snook, Texas during 1989, long-season, slower fruiting varieties resulted in less benefit of controlling a constant number of fleahoppers than

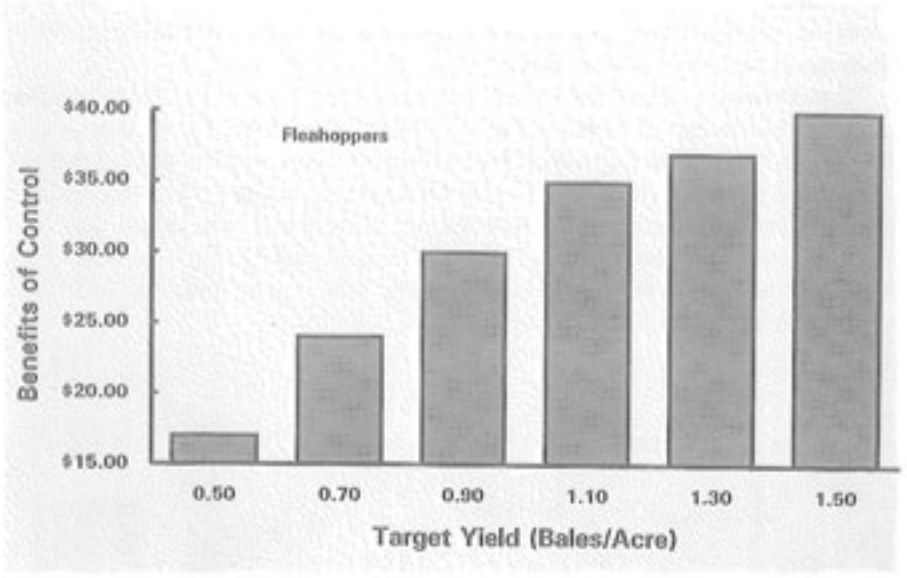

Figure 16. Benefits of controlling constant numbers of cotton fleahopper as a function of target yield.

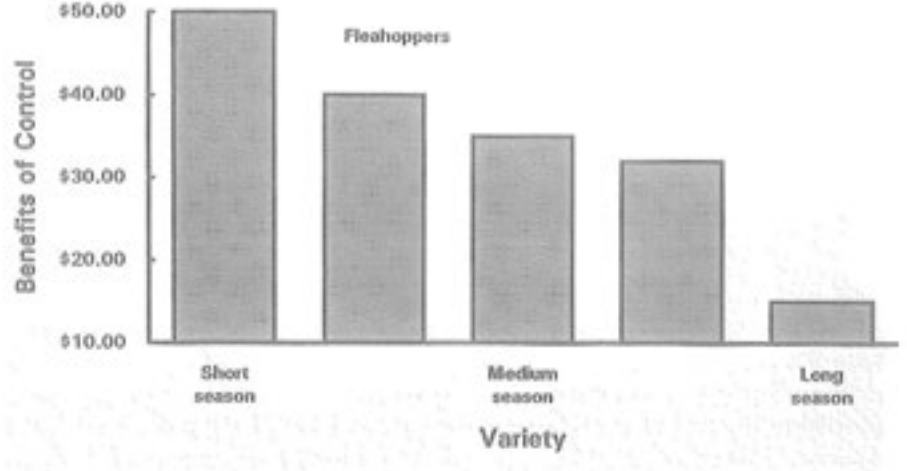

Figure 17. Benefits of controlling constant numbers of cotton fleahopper as a function of variety dependent on fruiting rate.

short-season, rapidly fruiting varieties. One reason for this difference is that long-season varieties generally have a greater ability to compensate for squares injured by fleahoppers than short-season varieties.

Plant Density — Plant density will also influence the amount of shade affecting immature boll weevil survival on the soil surface. To simulate the change in plant density, TEXCIM50 was run using Pecos, Texas historical weather data and 15 percent weevil injured squares entered three weeks after first square. Medium numbers of predators were entered together with average planting and harvest dates for Pecos. Plant densities were changed from 10 to 90 thousand plants per acre in TEXCIM50 while boll weevil numbers were held constant. This change increased benefits of boll weevil control by $12.97 per acre (Figure 18).

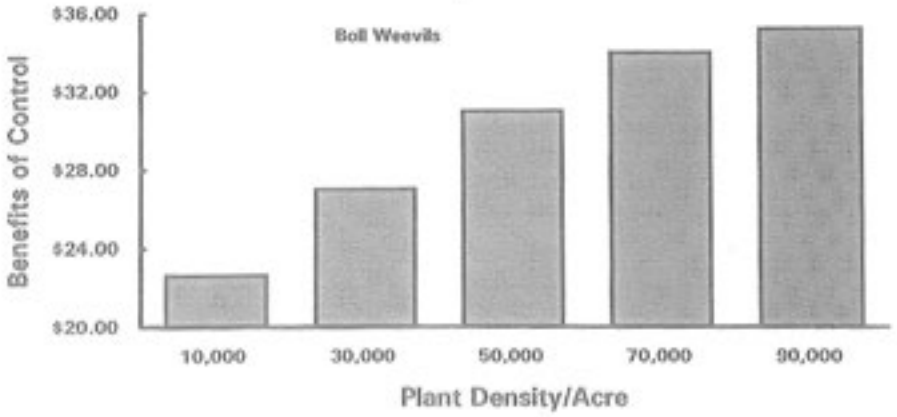

Figure 18. Benefits of controlling constant numbers of boll weevil as a function of plant density at Pecos, Texas.

Predator Numbers — The number of predators capable of checking the abundance of a pest and preventing economic loss has been called the inaction level for predators (Sterling, 1984). Inaction levels in current use in Texas include the density of predators able to prevent economic losses on boll weevil and bollworm-tobacco budworm (Knutson *et al.*, 1993). Models that consider the impact of predators include the various versions of TEXCIM, and another by Gutierrez and Baumgaertner (1984). The economic impact of native predators on cotton fleahoppers was estimated by Sterling *et al.* (1992).

By changing both the numbers of bollworm eggs and predator numbers, the benefits of bollworm control can be calculated. As predator numbers increase, the benefits of natural control also increase (Figure 19). However, predators alone do not determine the benefits of bollworm control. This benefit of control is, in part, a function of bollworm egg density and all other factors used by TEXCIM50 for forecasting benefits. Thus, an inaction level based on predator numbers alone is no more valid for forecasting benefits of control than pest numbers alone. Predators are simply one more component necessary for accurate forecasts.

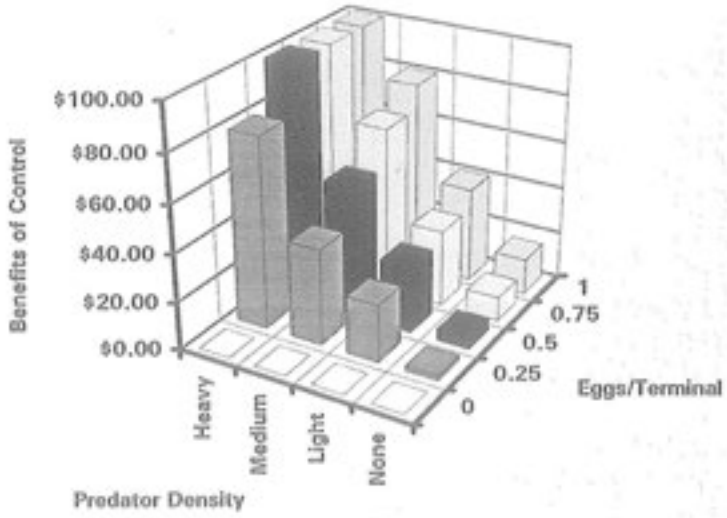

Figure 19. Benefits of controlling changing bollworm egg numbers as a function of predator density.

Pest Abundance — The abundance of an insect (or its injury) are imperfect predictors of yield loss (Pearson, 1958). However, insect numbers and injury are important components of a model designed to forecast benefits of control.

Using weather and predator data from Snook, Texas, fleahopper numbers were varied from one to eleven in increments of two. These fleahoppers were entered at the time of first square only. Under the conditions at Snook, the benefits of fleahopper control increased dramatically from about $10.00 per acre with one fleahopper per 3.3 feet to about $75.00 with 11 fleahoppers per 3.3 feet (Figure 20). Under the conditions of this simulation, TEXCIM50 was very sensitive to fleahopper abundance.

Multiple Pests — Using single species economic thresholds in cotton fields containing multiple pests results in a theoretical situation where a single fruit may be destroyed by several species concurrently. This is a case of contemporaneous (occur-

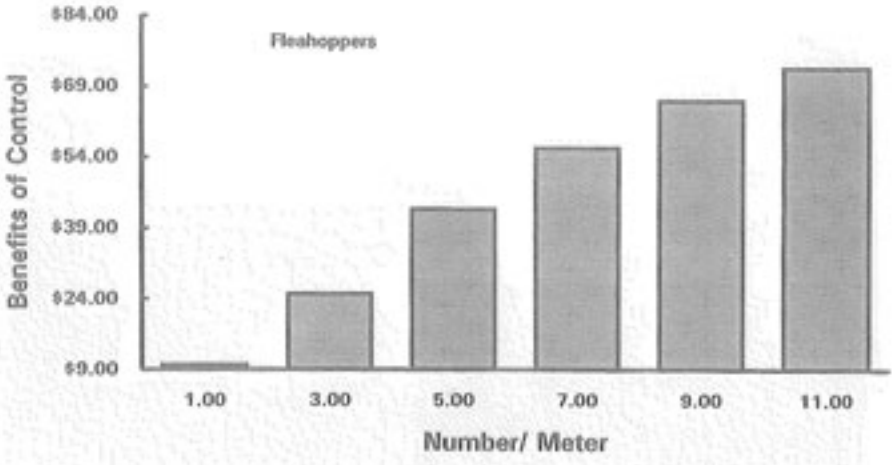

Figure 20. Benefits of cotton fleahopper control as a function of changing fleahopper densities.

ring at the same time) fruit mortality (Morris, 1965; Royama, 1981) where there is a tendency to overestimate concurrent injury caused by each pest (p. 491, National Academy of Sciences, 1969).

Using Snook, Texas data, when bollworm are run by themselves, the seasonal benefits of control were $20.72. When they were run simultaneously with fleahopper and boll weevil, the benefits of controlling the bollworm was $9.47. This suggests that simple economic thresholds based on single pests may tend to overestimate economic loss by that pest. The benefits of controlling a single pest is also a function of the damage caused by other pests. Part of the explanation for this phenomenon is that fruit feeding insects compete with each other so that when several are present, each one injures less fruit resulting in a lower benefit of control.

Most of the simple economic thresholds are based on research or practical experience designed to assess the effect of a single pest on yield. Methods to assess the impact of each of several pests simultaneously have not been available for use by farmers in cotton crop production. TEXCIM50 and TEXCIM for Windows currently provide essentially the only practical method for partitioning the economic benefits of controlling each pest in a multipest situation.

Insecticide Resistance or Insecticide Efficacy — Using TEXCIM50, cypermethrin (Ammo®, Cymbush®) insecticide was entered in a single application on June 3, 1989 on naturally occurring bollworms in the Snook, Texas, untreated cotton

field. The efficacy of cypermethrin was changed in 5 percent increments starting at 80 percent and ending at 100 percent. For simplicity, the assumption was made that cypermethrin was equally effective on eggs, small larvae and large larvae. The benefits of controlling bollworm as resistance to cypermethrin increases was simulated by reducing its efficacy. The efficacy of cypermethrin against predators was held constant at 95 percent.

A reduction in efficiency from 100 percent to 80 percent resulted in an increased benefit of bollworm control of $15.18 per acre (Figure 21). Thus, benefits of bollworm control from a single application of cypermethrin had a dramatic effect under conditions at Snook, Texas when the level of efficacy changed. The benefits of bollworm control declined rapidly as a function of increased insecticide efficacy. These results are counterintuitive and no ready explanation for them is available.

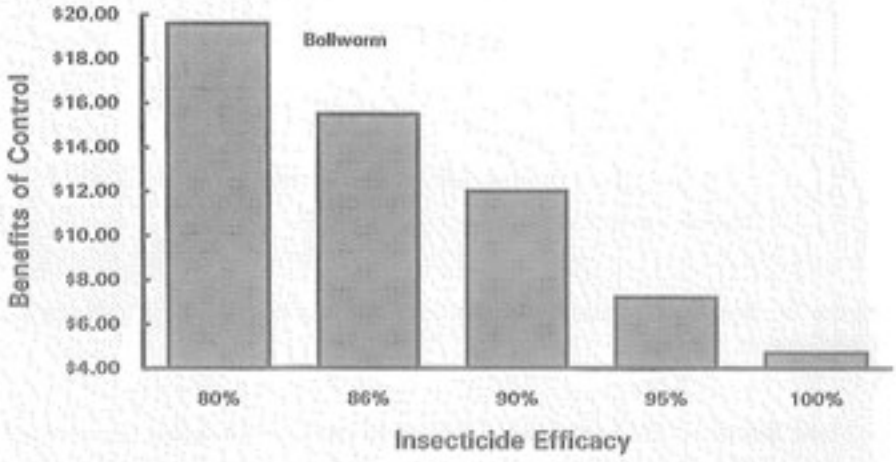

Figure 21. Changes in the benefits of bollworm control as a function of changes in the efficacy of cypermethrin.

Timing of Insecticide Applications — The use of models to evaluate different insecticidal application regimes has been conducted on an earlier version of the boll weevil component of the TEXCIM50 model (Talpaz *et al.*, 1978). The timing of insecticides to coincide with susceptible stages of pests is critical in pest management programs. As the efficiency of an insecticide changes when applied at different times, the benefits of control must also change. When a single application of cypermethrin was made at different times starting on June 19 and ending on July 14,

the benefits of bollworm control changed (Figure 22). Bollworm egg and larval numbers peaked on July 7 at Snook, Texas.

If the efficiency of an insecticide was reduced through improper timing, the benefits of control increased. Conversely, if efficiency increased, the economic benefits decreased.

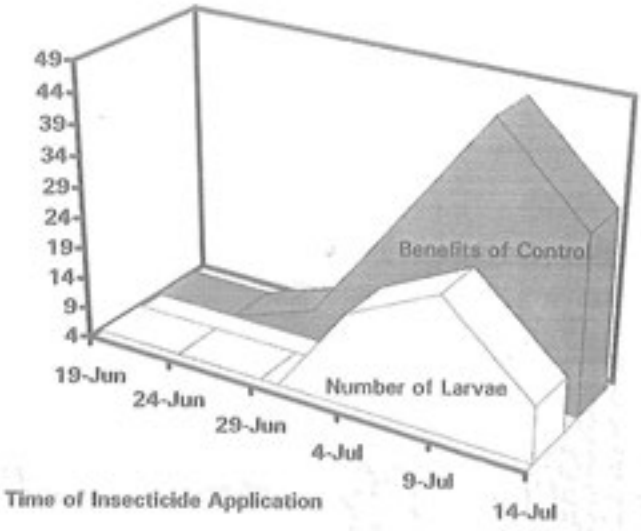

Figure 22. Benefits of bollworm control as a function of the time of cypermethrin application.

Plant Stress — Graham *et al.* (1972) recommended changing the economic threshold based on variations in plant susceptibility to insect injury. Other factors affecting plant stress such as weeds, diseases, nematodes, water and nitrogen will interact with all other factors that affect economic decisions. Multiple component, pest management models of the future will require attention to other factors to improve the accuracy of forecasts. TEXCIM for Windows does not currently include weed, disease or nematode components that impose a stress on the plant. However, the ICEMM model (Landivar *et al.*, 1991) can evaluate stresses due to nitrogen, water and plant growth regulators simultaneously with pest injury.

Sampling Method — The sampling method used to provide information on pest numbers, fruit numbers, predators and weather can have an impact on the accuracy of economic forecasts. In general, field counts of bollworm larvae result in less forecasting error than counts of eggs (Figure 23). Counts of bollworm (BB) moths or boll weevil (WV) adults monitored in pheromone traps result in higher forecasting

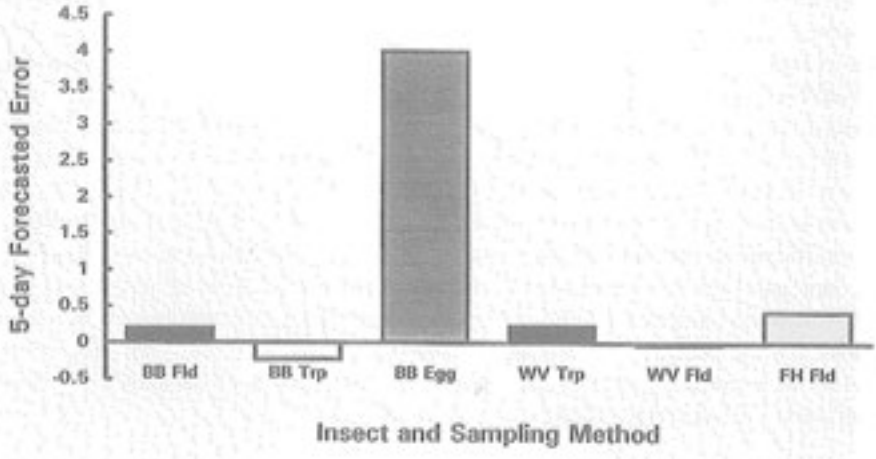

Figure 23. Forecasting errors based on initializing TEXCIM50 with counts of pests based on different sampling techniques. Abbreviations are BB = bollworm/budworm, FLD = field, TRP = trap, WV = bollweevil and FH = fleahopper.

errors than field counts of fruit injury and immatures (Sterling *et al.*, unpublished). Thus, a very accurate model may produce forecasts with considerable error if based on data obtained from unreliable samples.

Relation Between Sampling Method, Forecasts and the Economic Thresholds — The decision to control pests is a function of the sampling method and time. For example, the purpose of sampling boll weevil in pheromone traps is to forecast the consequences of immediate boll weevil control to prevent economic injury one or two months into the future. The idea is to control overwintered boll weevils in the spring before they have a chance to reproduce. Thus, the growth rate of boll weevil populations is reduced so that, after one or two generations, insufficient numbers of boll weevils are present to require control during mid-season. Thus, economic thresholds based on trap catches function as a forecasting model. For all models, forecasting error increases with distance into the future. However, when considering the alternatives of using the boll weevil trapping index or the TEXCIM50 model to forecast current benefits of control, the limitations of the trap index as a forecasting model become obvious. Since the trap index does not consider weevil mortality, weather and plant growth, etc. it cannot possibly provide consistently accurate forecasts and thus should be used with considerable caution. With continuous testing and revision, the TEXCIM50 approach should ultimately lead to much improved forecasts and management decisions.

In taking field counts of fleahoppers during the growing season, the goal may be to make a control decision based on a forecast in the next 5 or 10 days. However, when sampling bollworm with pheromone traps, the goal may be to make a decision based on a longer forecast of 10-15 days, depending on how long it takes the moths to colonize the field and lay eggs that produce large larvae. Thus, a crop manager would not make a decision to treat today based on pheromone trap catches of moths taken today. However, he could plan to take actions in about 10 days based on forecasts of 10 to 15 days. The decision to control boll weevil depends on the management strategy. If the strategy is to control overwintered boll weevil to prevent them from increasing to numbers that would cause injury in the third or fourth generation, then long-term forecasts of much more than 25 days may be necessary. However, if a forecast of the first generation is adequate, then a forecast of 25 days may be sufficient. The main point is that at times, moderately long-term forecasts may be desirable, but the accuracy of forecasts declines over time (Sterling *et al.*, unpublished data). The most accurate decisions are obtained with field samples of insects or injury rather than trap catches.

EXTERNALITIES AND THEIR COSTS

When insecticides are used in a cotton field, the farmer does not pay all the costs of application. Pesticides often enter the ground or surface water where they may affect the health of others who may drink the water. These are the so-called "side effects" of insecticide use. DDT apparently moves in wind and water currents over much of the surface of the world causing harm to many biological organisms. TEXCIM50 currently makes no attempt to include external costs as part of the costs of pest control. Currently, farmers are paying some of the costs of these externalities with higher taxes to support agencies such as the Environmental Protection Agency and through higher insurance premiums to cover potential litigation resulting from the use of chemical control. We assume that farmers pay only a small fraction of the true external costs. Estimates of external costs of applying a single insecticide range from $0.91 to $4.67 per acre (Higley and Wintersteen, 1992). These costs include costs to surface water, ground water, aquatic environment, birds, mammals, beneficial insects, human acute toxicity and human chronic toxicity. These costs can be expected to vary from field to field depending on many factors. It will be very difficult to accurately calculate these costs for each cotton field. However if such an estimate is available it can be included in the total costs of control. Also, all of these costs are not external. A fraction of these costs are borne by the farmer. Because the farmer, his family or his employees either live or work in close proximity to the application site, they are most likely to receive major exposure to insecticides. Thus, the farmer is paying for some of this exposure in higher medical bills or in the reduced efficacy of natural enemies, whether he knows it or not. It is probably not valid to assume that the farmer pays no part of these costs.

SIMPLICITY

One of the major advantages of the simple economic threshold is its simplicity (Pedigo *et al.*, 1986). However, there are other criteria such as reliability, value and objectivity that may be of considerable importance. Granted, many pest managers may refuse to use a system because of its complexity, but pest managers may also lose confidence in systems with high failure rates over the long term. Failure of pest management systems may frequently be due to a shortage of reliable information. However, systems which are accurate and provide a satisfactory return on the investment in labor will be used if they are consistently reliable. Farmers make money by either increasing yields more than costs or reducing costs and holding yields at near the same level. Thus, knowing when to treat and when not to treat can both return a profit. If this profit is sufficient it will cover the cost of acquiring knowledge and models such as TEXCIM50 will prove to be a good investment. Since farmers tend to be averse to risk (Norgaard, 1976), objective, accurate systems will soon gain the confidence of farmers if the known risks are lower than subjectively perceived risks and if consistent profits result from using the models. A distinguishing feature of these models is that they introduce greater objectivity into the decision-making process.

LIMITATIONS OF TEXCIM

The plant model contained in TEXCIM50 and TEXCIM for Windows is a simple fruit dynamics model that is not based on plant physiology. It is designed to produce fruit as a function primarily of temperature. Each fruit is assigned an economic value that changes as the fruit grows and matures or is injured and lost from the crop. Integrating insects into this system that function as stand reducers, leaf-mass consumers, assimilate sappers or turgor reducers would be difficult using this fruit model. TEXCIM for Windows has been integrated with (TEXCOT) (Unpublished data, J. A. Landivar, Texas A&M University, Corpus Christi, Texas) a version of the GOSSYM physiologically based plant model (Baker *et al.*, 1983) to form the ICEMM model (Landivar *et al.*, 1991). This model facilitates the linkage of these pests to carbon, nitrogen and water contents (pools) in the plant.

SUMMARY

Pest numbers or pest injury alone cannot provide consistently accurate forecasts of costs, benefits and profits of pest control. Thus, the simple economic threshold that depends on pest numbers or pest injury alone cannot be consistently reliable in making pest management decisions. Using the TEXCIM for Windows and related models, pest management decisions are based on a profit analysis of potential management tactics. If forecasted benefits of control equal the costs of control, then the economic threshold has been reached. Anything that changes plant growth rates, yield potential, or economics of crop production will change the economic threshold. Because plant growth rates, yield potential and economics of crop production are different in every cotton field, management decisions based on a single criterion, such as pest density

cannot provide accurate decision criteria in all cotton fields. As used in TEXCIM, the comprehensive economic threshold does not depend on pest numbers or their injury alone, it is a function of all costs, benefits and profits of control. Evidence is provided of the need for many factors — time of attack, geographical location, lint value, planting date, harvest date, row width, row orientation, target yield, plant variety, plant density, predator numbers, pest numbers, multiple pests, resistance, timing, stress and sampling — in determining forecasted benefits of pest control. No single factor such as pest numbers, lint value and predator numbers can provide accurate criteria for making management decisions. The TEXCIM model provides an example of an analytical tool useful in forecasting the profitability as needed for scientific pest management and for partitioning the economic benefits of controlling each pest when multiple pests are simultaneously attacking the crop.

Although forecasting the profitability of insect control separately for each cotton field may result in more reliable decisions than extrapolations from a single run for a community, in practice the forecasts for a single variety planted simultaneously on a farm or fraction of a community may sometimes be practical. Errors in long-term forecasts are greater than in short-term forecasts so economics should be most reliable with short-term forecasts. Ultimately, the use of this information will be based on its value to the farmer or his crop manager. The crop manager will ultimately make management decisions based on returns exceeding the investment in pest control. Improvements in the accuracy of economic thresholds should result in sufficient benefit to the farmer to more than justify the cost of data acquisition (sampling) needed to run the model. This information may serve to reduce the cost of other technologies, such as insecticides, to provide an acceptable return on the investment in sampling to obtain the information. Accurately determining costs, benefits and profits of control may play a key role in reducing the risks of making unprofitable treatment decisions or unprofitable decisions not to treat.

ACKNOWLEDGMENT

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Chapter 8

TOXICOLOGY OF INSECTICIDES AND ACARICIDES

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INTRODUCTION

The history of insect control on cotton since World War II can be divided into three periods based on the types of insecticides used to control the major cotton insect pests such as the tobacco budworm, *Heliothis virescens* (F.), the bollworm, *Helicoverpa zea* (Boddie) and the boll weevil *Anthonomus grandis grandis* Boheman. The first period was the DDT and organochlorine period, lasting from their introduction just after World War II to the mid- 1960s when widespread resistance and environmental concerns began to outweigh benefits derived from their continued use (Sparks, 1981; also see Chapter 13). The second period was that of the organophosphorus insecticides as exemplified by methyl parathion which came into prominent use as the utility of DDT and other organochlorines declined during the mid-1960s. Although still widely used for control of some cotton insect pests, the organophosphorus insecticide period of predominance declined during the late 1970s when the tobacco budworm developed resistance to many of the organophosphorus insecticides then in use (Sparks, 1981; Sparks *et al.*, 1993a) and the third period, that of the pyrethroid insecticides, began. Currently, pyrethroids are the predominant insecticides used for the control of the primary cotton insect pests such as the bollworm/tobacco budworm. However, because pyrethroid resistance is now present in many parts of the United States (Martinez-Carrillo and Reynolds, 1983; Nicholson and Miller, 1985; Miller, 1987; Campanhola and Plapp, 1987; Leonard *et al.*, 1987, 1988a; Luttrell *et al.*, 1987; Graves *et al.*, 1988; Sparks *et al.*, 1993a; also see this volume), we may be entering a new period of cotton insect control.

Interest in insecticide-related research on cotton insects, as measured by the percentage of publications devoted to the subject in the Journal of Economic Entomology, has fluctuated over the last 40 years (Figure 1). In part, these fluctuations may result from problems with insecticide resistance, environmental concerns and the periodic introduction of new chemistry. For example, the peaks that occur in the mid-1950s correspond with the development of insecticide resistance in the boll weevil, while those in the mid-1970s occur at the time of organophosphorus insecticide resistance appearing in the tobacco budworm and the introduction of pyrethroid insecticides (Sparks,

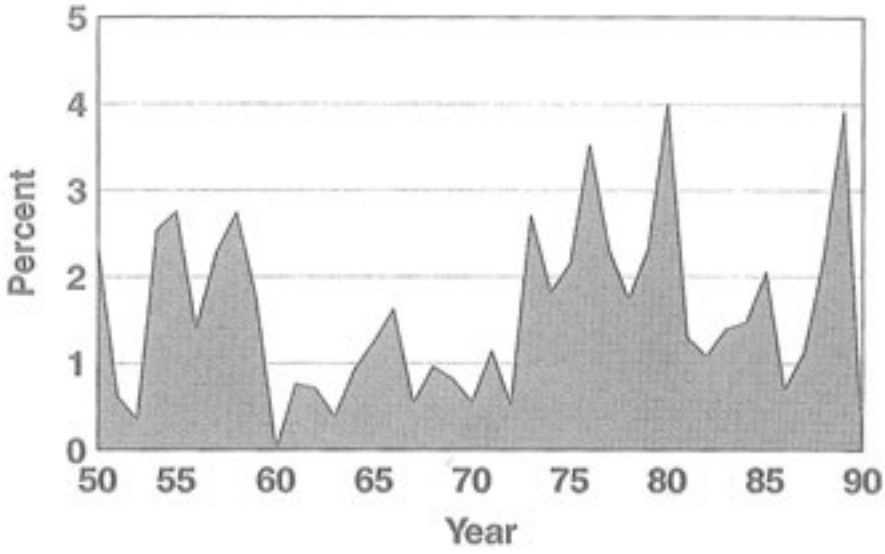


Figure 1. Percentage of articles on the interaction of cotton insects with insecticides (toxicity, metabolism, field efficacy, etc.) published each year in the Journal of Economic Entomology.

1981). The recent peak for 1987-1990 may also reflect the increasing concern over pyrethroid resistance in cotton insects (Sparks *et al.*, 1993a).

Cotton insect control has undergone an evolution from a strictly chemical- based system, to a system of insect pest management, and to what is now being termed resistance management. The appearance of resistance management (National Research Council, 1986) as a concept, reflects the realization that the arsenal of insecticidal compounds for use on cotton or any other crop, is very definitely limited, especially given the increasing concern for the environment, human and animal safety, and the increasing cost of insecticide discovery and development (Georghiou, 1986; Hammock and Soderlund, 1986). Therefore, currently registered and available compounds should be treated as valuable, potentially non-renewable resources, that we can ill afford to lose or waste.

Central to implementing any resistance management program, as well as the successful and safe use of current and future insecticides, is the need to understand the modes of action and mechanisms of detoxification and activation of the insecticide involved. Whole books have been devoted to the subject of insecticide and miticide toxicology (O'Brien, 1967; Brooks, 1974; Eto, 1974; Kuhr and Dorough, 1976; Wilkinson, 1976a; Coats, 1982; Corbett *et al.*, 1984; Matsumura, 1985; Hutson and Roberts, 1985; Kerkut and Gilbert, 1985; Wright and Retnakaran, 1987; Crombie, 1990; Duce, 1992; Duke *et al.*, 1993). This chapter is not intended to provide an exhaustive review of insecticide toxicology, rather the intent is to provide an overview

of insecticide chemistry, mode of action and metabolism within the framework of the cotton pest complex. Given the scope of this book in general and this chapter in particular, many of the lesser insecticide groups will not be considered and the reader is directed to more comprehensive texts for information on these subjects (Corbett *et al.*, 1984; Matsumura, 1985; Kerkut and Gilbert, 1985).

CLASSIFICATION AND MODE OF ACTION

The first critical problem in discussing the toxicology of such a diverse group of compounds is to provide a framework for the reader. Several classification approaches are possible including those based on chemistry, mode of action, origin and method of discovery. The review provided herein will be based on a combination of chemistry and mode of action. A classification based strictly on chemistry can be misleading or allow important connections to be lost. For example, in spite of what appears to be radically different chemistry, DDT and the pyrethroids have the same site of action and the same primary resistance mechanism (knock-down resistance). In fact, in many respects, DDT can be considered the first pyrethroid. Likewise, generally accepted chemical groupings such as the chlorinated hydrocarbon insecticides, which usually consist of DDT and its analogs, the cyclodienes and lindane, are usually treated as a group, and yet they are vastly different in terms of chemistry, mode of action and resistance.

Although not generally viewed as such, almost all modern insecticides can potentially be viewed as has having one of two broad modes of action. The first is to mimic or enhance the action of an endogenous (inside the organism) molecule such as a neurotransmitter, while the second is to block or antagonize the action of an endogenous molecule (Table 1). For example, the organophosphorus insecticides can be thought of as functioning by inhibiting acetylcholinesterase which allows increased levels of acetylcholine to stimulate the postsynaptic acetylcholine receptors. Thus, in one sense, the organophosphates can be viewed as having the same effect as mimicking the action of acetylcholine. Similar examples can potentially be made for the carbamates, cyclodienes and pyrethroids (Table 1).

Obviously, this view point has its limitations. Like any classification system, there are difficulties with insecticides that have unclear modes of action, those that act as general metabolic poisons or that act on a variety of systems. This point of view also can become overly simplistic when there is a change in the function or large fluctuations in the titer (chemical balance) of the target compound during the course of the insect's development. While neurotransmitters such as acetylcholine and *gamma*-aminobutyric acid perform the same function throughout the life of the insect, hormones such as juvenile hormone, and perhaps some of the neurohormones, regulate a variety of functions depending on the particular life stage involved. However, keeping this limitation in mind, this approach will hopefully result in a better grasp of the ultimate site of action at the biochemical level.

A majority of the insecticides in use today, including the pyrethroids, the cyclodienes, the organophosphates, carbamates, avermectins, formamidines and nicotinoids, act via the

Table 1. Mode of action of insecticides and acaricides

Insecticide	Target site	Ultimate target				
		Mode of action	Mimic	Antagonist[1]	Endogenous compound	System
DDT & Pyrethroids	Na+ Gate	Open Na+ gate		*	ACh	Nervous
Nicotine	ACh Receptor	Block ACh receptor		*	ACh	Nervous
Nitromethylenes	ACh Receptor	Block Ach receptor	*		ACh	Nervous
Cyclodienes & Phenylpyrazoles	GABA Cl- channel	Block GABA, Stimulate ACh release	*		ACh	Nervous
Organophosphates	AChE	Inhibit AChE	*		ACh	Nervous
Carbamates	AChE	Inhibit AChE	*		ACh	Nervous
Formamidines	Octopamine receptor	Mimic Octopamine	*		Octpamine	Nervous
Avermectins	GABA Cl- channel	Increase GABA binding	*		GABA	Nervous
Rotenone	Electron transport	Block malate oxidation		*	ATP	Energy
Dinitrophenols & Pyrroles	Mitochondrial uncoupler binding site	Uncouple ATP production		*	ATP	Energy
Sulfur containing miticides	Mitochondiral ATPase	Inhibition of oxidative phosphorylation		*	ATP	Energy

Table 1. Continued

Benzoylphenyl ureas	Chitin synthesis	Block chitin synthesis	NA[2]	NA	Chitin	Structure
Diacylhydrazide	Ecdysone Receptor	Mimic edcysone	*		Ecdysone	Endocrine
Juvenoids	JH receptors	Mimic JH	*		JH	Endocrine
Anti-JHs	JH biosynthesis in CA	Block JH production		*	JH	Endocrine
Bacillus thuringiensis	Gut epithelium	Disruption of gut-hemolcoel barrier	NA	NA	NA	Structure

Abbreviations used: ACh - acetylcholine; AChE - acetylcholinesterase; CA - corpora allata; GABA- *gamma*-aminobutyric acid; JH - juvenile hormone

[1]Antagonize or block action of endogenous compound
[2]Not applicable

insect nervous system (Matsumura, 1985; Table 1). This is because the nervous system of insects, as well as that of mammals, is regulatory in function. Minute changes or disruptions are greatly and rapidly amplified, quickly leading to a breakdown in the system. The nervous system will most likely remain a primary target for new insecticides, as demonstrated by the avermectins. However, other regulatory systems in insects such as the endocrine system may also prove to be good target sites for insecticide action (Sparks, 1990), especially at the neuroendocrine (hormonal system affecting the function of the nervous system) level (O'Shea, 1985, 1986; Holman *et al.*, 1990; Masler *et al.*, 1993).

INSECTICIDE MODE OF ACTION

Although cotton insect control traditionally has accounted for a large proportion of the insecticides used in the United States, cotton insect pests such as the tobacco budworm have not typically been used in studies involving mode of action or structure-activity relationships. In most instances our knowledge concerning insecticide mode of action and structure-activity relationships comes from studies on insects such as the house fly. Likewise, except in selected areas, our knowledge of the basic biochemistry of cotton insect pests is relatively limited. The following overview of insecticide mode of action will be limited to the more important insecticide classes, and where possible, include information derived from studies using cotton insect pests.

DDT AND THE PYRETHROIDS

Although generally viewed as belonging to different insecticide classes, DDT and the pyrethroids share the same mode of action and resistance mechanisms. While DDT and the pyrethroids appear to be quite different chemically (Figure 2), the continual evolution of pyrethroid and DDT chemistry has led to compounds that are DDT-pyrethroid intermediates (Holan *et al.*, 1985). Thus chemically, DDT and the pyrethroids may merely represent opposite ends of a spectrum of compounds that all have the same site of action.

Although DDT, the natural pyrethrins and pyrethroids have been the subject of more than 40 years of research, their exact mode of action and target site requirements still present many unanswered questions. This is in spite of the vital role in agriculture that DDT used to play and that the pyrethroids have largely taken over.

DDT and the pyrethroids act within the central nervous system to disrupt axonal transmission of nerve impulses in insects and mammals (Lund, 1985; Matsumura, 1985; Soderlund and Bloomquist, 1989) and, as an ultimate consequence, disrupt the transmission of information through the axon ultimately disrupting the release of acetylcholine (Table 1). In a nerve axon the passing of a nerve impulse temporarily disrupts the sodium gradient normally present. This change in the sodium gradient results from the rapid opening of the sodium gates leading to a rapid depolarization of the nerve. Although DDT and the pyrethroids are known to affect a variety of systems (Miller and Adams, 1982; Osborne, 1985; Ruigt, 1985), it now appears that the central factor in their action is the disruption of nervous transmission in the central nervous

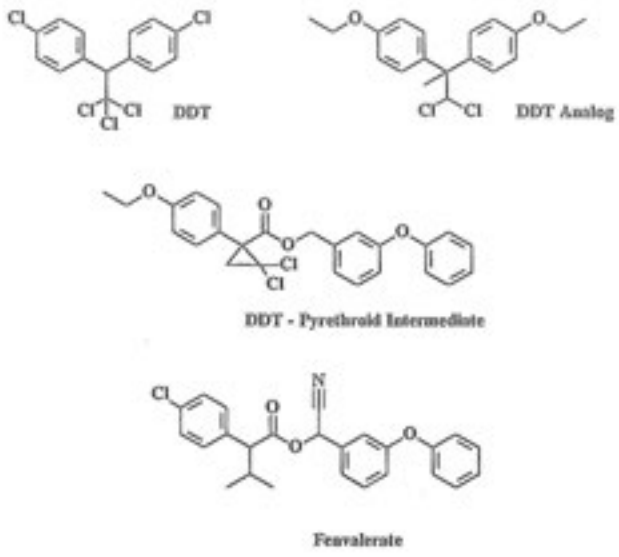


Figure 2. Structures of DDT, a DDT analog (Abu-El-Haj *et al.*, 1979), a DDT-pyrethroid intermediate (Holan *et al.*, 1985) and the pyrethroid fenvalerate.

system (Narahashi, 1987; Soderlund and Bloomquist, 1989). This disruption appears to be the direct consequence of DDT and the pyrethroids binding to voltage gated sodium channels, thereby preventing them from closing properly and leading to a continuous depolarization of the nerve (Matsumura, 1985; Ruigt, 1985; Suderlund and Bloomquist, 1989).

Although possessing the same target site, the actions and symptoms of DDT and the pyrethroids have often been divided into two groups: Type I and Type II. There are several distinctions between these two groups including the generation of repetitive discharges and characteristic whole body tremors by the DDT and the Type I pyrethroids versus a lack of these features by the Type II pyrethroids (Gammon *et al.*, 1981; Matsumura, 1985; Soderlund and Bloomquist, 1989). Type I pyrethroids typically would include the natural pyrethrins, DDT, and the non-*alpha*-cyano pyrethroids, phenothrin and permethrin (Pounce®, Ambush®), while the Type II pyrethroids usually include *alpha*-cyano pyrethroids such as cypermethrin (Ammo®, Cymbush®), fenvalerate (Pydrin®) and deltamethrin (Decis®).

Effects of Temperature — Although generally viewed as increasing in toxicity with decreasing temperature (negative temperature coefficient), recent studies suggest a much more complex relationship. Relative to the tobacco budworm, DDT and the Type I pyrethroids, permethrin and phenothrin, all possessed large negative temperature coefficients, while the Type II pyrethroids, fenvalerate, cypermethrin, deltamethrin

and tralomethrin (Scout®), all possess slightly negative or positive temperature coefficients (Sparks *et al.*, 1983). Based on the results of several studies (Sparks *et al.*, 1982, 1983; Schmidt and Robertson, 1986; Toth and Sparks, 1988, 1990) the response of pyrethroid toxicity to temperature is affected, in part, by the insect species being tested, the pyrethroid being evaluated, the method of application and the temperatures used in the evaluation. Thus, caution should be exercised in relating the effects of temperature on pyrethroid toxicity in the laboratory directly to a field situation.

DDT — DDT was a major component in the control of bollworm/tobacco budworm and the boll weevil during the 1950s and into the early 1960s. Compared to many carbamate and organophosphorus insecticides, DDT possesses good activity against cotton insect pests such as the tobacco budworm (Table 2). Studies of DDT and its structural requirements for activity suggest that the DDT molecule must fit onto a receptor site for which there exist strict size requirements (Coats, 1982; Fukuto and Keadtisuke, 1992). While DDT possesses good activity, there exist other structural variations that also display high biological activity (Coats, 1982; Fukuto and Keadtisuke, 1992). For larvae of the tobacco budworm, the toxicity of many of the pyrethroids is orders of magnitude higher than DDT.

Pyrethroids — As with DDT and its analogs, there also appears to be rather strict structural requirements for good biological activity in the pyrethroids (Elliott, 1985, 1990; Yoshioka, 1992). Due to the complex chemical nature of the pyrethroids, the structural requirements for activity are difficult to define. Most commercial pyrethroids are made up of an alcohol and an acid usually joined by an ester linkage (Figure 3). In the acid, a cyclopropane ring possessing gem dimethyl groups and an unsaturated sidechain (typically 2,2-dihalovinyl), are generally necessary for high activity (Buchel, 1983). Newer pyrethroids such as fenvalerate (Pydrin®) and fluvalinate (Mavrik®) maintain a configuration in the acid similar to the gem dimethyls on the cyclopropane ring by substituting an *alpha*-(1-methylethyl)benzeneacetic acid (Figure 3). In the alcohol a planar ring structure such as benzene or furan with an unsaturated sidechain or benzene ring seems to be necessary. Continued research on pyrethroid chemistry has resulted in the development of a number of non-ester linked pyrethroids (Udagawa *et al.*, 1985; Bushell, 1990; Sieburth *et al.*, 1990; Yoshioka, 1992) that may eventually find application to cotton insect control.

Much of the effort that has gone into detailing the requirements for pyrethroid activity have also dealt with improving environmental stability, since early pyrethroids such as allethrin, were broken down far too rapidly in an agricultural setting to be of use. Permethrin (Pounce®, Ambush®) was the first pyrethroid to truly be successful in an agricultural setting and was quickly followed by a host of other compounds (Elliott, 1977, 1985, 1990). Relative to permethrin, the first pyrethroid available for widespread use in cotton, other widely used pyrethroids are from 2 to nearly 30 times more toxic to the tobacco budworm in topical bioassays (Table 2). More importantly, most pyrethroids are much less toxic to mammals than are many of the organophosphorus insecticides, such as methyl parathion, that they replaced (Table 2).

Table 2: Toxicity of selected cotton insecticides and acaricides.

Compound	Toxicity (LD_{50} or LC_{50}) Tobacco budworm (mg/g)	Bollworm (mg/g)	Boll weevil (mg/weevil)	Twospotted spider mite (ppm)	Rat oral (mg/kg)
DDT & PYRETHROIDS					
DDT	31.5-100.0	30-82	—	—	87
Biphenthrin	1.32	0.71	—	46	55
Cypermethrin	0.241-1.61	1.96	0.2	185	247
Cyfluthrin	1.00	—	—	—	590
lambda-Cyhalothrin	0.929	1.11	—	—	56
Deltamethrin	0.044-0.107	0.071	0.033	287	128
Esfenvalerate	0.429	—	—	—	75
Fenpropathrin	0.51	—	0.36	241	49
Fenvalerate	0.396-1.89	2.64	0.71-0.477	142	451
Flucythrinate	0.254	—	—	266	67
Fluvalinate	1.89	—	—	121	>6,299
Permethrin	1.33-2.79	1.00	0.053	319	>4,000
Phenothrin	2.51	0.770	1.53	—	>10,000
Tralomethrin	0.061	—	—	—	1070
ORGANOPHOSPORUS INSECTICIDES					
Acephate	41.0-74.3	—	>5700.0	—	886
Azinphosmethyl	29.33	14.0	0.062	240	5
Chlorpyrifos	79.5	—	—	3352	135
EPN	37.0	5.67	0.20-0.04	—	14
Malathion	2230.0	150.0	0.66-1.24	3542	885
Methamidophos	85.7-150.0	150.0	128.6	—	13
Methyl Parathion	8.33-20.0	5.67-20.0	0.047-0.061	8112	9
Monocrotophos	29.67	6.00	0.42-1.34	—	21
Profenofos	11.0-11.8	0.07	0.53	234	400
Sulprofos	24.0-25.6	11.3	1.27	—	107
CARBAMATES					
Aldicarb	571.0	—	0.22	21	1
Carbaryl	183.3	193.3	27.7-48.9	—	307
Carbofuran	—	—	0.057	—	8
Methomyl	4.33-30.0	7.00	—	300	17
Thiodicarb	200.0	—	—	—	1,600
FORMAMIDINES					
Amitraz	—	—	—	139	600
Chlordimeform	>400.0	—	—	319	170

Table 2: Continued.

Compound	Toxicity (LD_{50} or LC_{50}) Tobacco budworm (mg/g)	Bollworm (mg/g)	Boll weevil (mg/weevil)	Twospotted spider mite (ppm)	Rat oral (mg/kg)
ACARICIDES					
Cyhexatin	—	—	—	94	180
Dicofol	—	—	—	5	575
Propargite	—	—	—	203	1,480
Tetradifon	—	—	—	127	>5,000
CYCLODIENES					
Endosulfan	73.3	156.7	—	—	18
Endrin	46.7	23.3	—	242	3
AVERMECTINS					
Abamectin	1.16	7.49	1.26	0.05-0.14[4]	10.6–11.3
MK-244	0.12	—	—	—	—
SPINOSYNS					
Spinosyn A	1.28	—	—	—	3783–>5000
PYRROLES					
AC 303,630	—	—	—	1.6[4]	662
CHLORONICOTINYLS					
Imidacloprid	350	—	—	—	450
PHENYLPYRAZOLES					
Fipronil	—	—	—	—	100
SYNERGISTS					
Piperonyl butoxide	>400.0	—	—	—	6,150
IGR'S					
Fenoxycarb	>400.0	—	—	—	16,800
FMev[1]	4000[3]	—	—	—	—
DPH[2]	276[3]	—	—	—	—

Tobacco budworm—Topical toxicity to third instar larvae: data adapted from Graves *et al.*, 1964; Adkisson and Nemec, 1967; Wolfenbarger and Guerra, 1972; Whitten and Bull, 1974; Harding *et al.*, 1977; Nosky *et al.*, 1980; Wolfenbarger and Harding, 1980; Polazzo, 1978; Sparks *et al.*, 1983; Rose and Sparks, 1984; Quistad *et al.*, 1985; Anderson *et al.*, 1986; Bull, 1986; Leonard *et al.*, 1988a,b; Lagadic and Bernard, 1993; Sparks *et al.*, 1995; R. Leonard and J. B. Graves Department of

Table 2: Continued.

Entomology, Louisiana State University, Baton Rouge; and D. Wolfenbarger, USDA, ARS, Weslaco, TX (unpublished data).

Bollworm—Topical toxicity to third instar larvae: data adapted from Graves *et al.* 1963, 1964; Adkisson and Nemec, 1967; Wolfenbarger and Guerra, 1972; Davis *et al.*, 1977; Polazzo, 1978; Bull, 1986; and Leonard *et al.*, 1988a.

Boll weevil—Topical toxicity to adults: data adapted from Hopkins *et al.*, 1975; Davis *et al.*, 1977; Harding *et al.*, 1977; Sparks *et al.*, 1983; Rose and Sparks, 1984; Wolfenbarger *et al.*, 1985.

Twospotted spider mite— Slide dip bioassay: data adapted from Chang and Knowles, 1977; Dennehy and Granett, 1984; Dennehy *et al.*, 1987; Knowles and El-Sayed, 1985; Hoy and Conley, 1987.

Rat oral data for technical material adapted from Buchel, 1983; Larson et al., 1985; Thompson, 1985; Anonymous, 1988; Addor *et al.*, 1992; Lankas and Gordon, 1989.

[1]Fluoromevalonolactone
[2]3,3-dichloro-2-propenyl hexanoate
[3]ED50
[4]Leaf-dip bioassay.

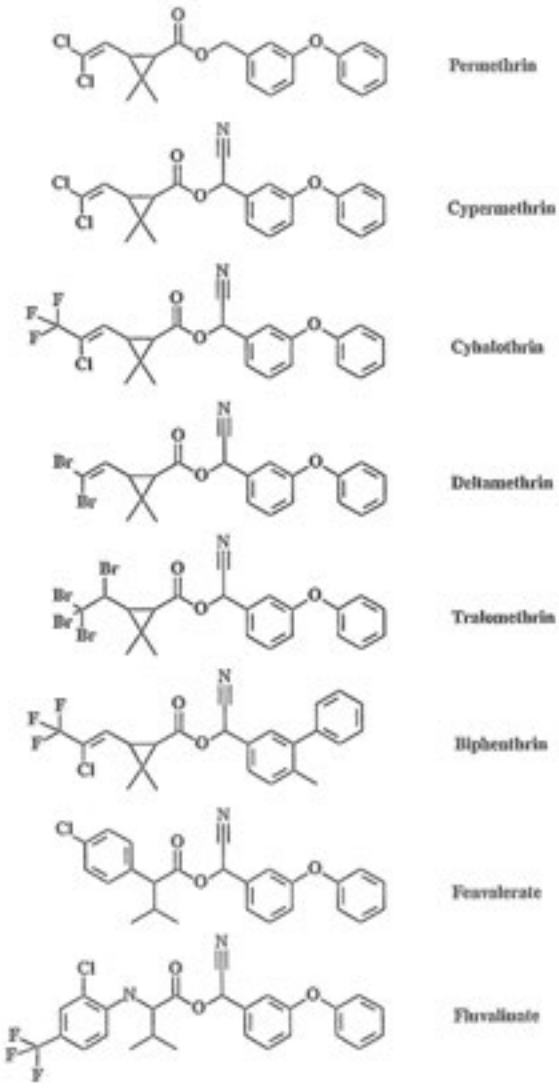


Figure 3. Structures of pyrethroids used for cotton insect control.

ORGANOPHOSPHORUS COMPOUNDS

A critical component of the insect central nervous system is the junction separating two nerve cells, the synapse. At the cholinergic synapse the action potential is translated

to packets of the neurotransmitter acetylcholine (Figure 4) that binds to receptors in the post-synapse causing a depolarization of that nerve cell and a continuance of the nerve impulse. The over stimulation of post-synaptic receptors by acetylcholine is prevented by the presence of an enzyme, acetylcholinesterase, that rapidly breaks down the acetylcholine (Figure 5) before an excess can accumulate at the post-synaptic receptors.

The heart of the active site of acetylcholinesterase, like other serine proteases and carboxylesterases, is a serine hydroxyl group in what is known as the esteratic site (Eto, 1974; Matsumura, 1985). The quartenary nitrogen of the choline group is bound

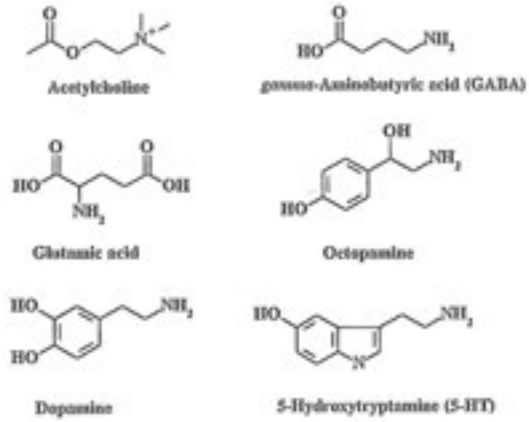


Figure 4. Structures of insect neurotransmitters.

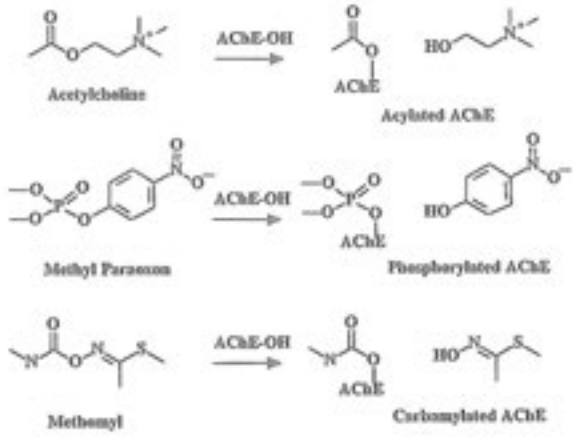


Figure 5. Interaction of acetylcholine, an organophosphorus insecticide (methyl paraoxon) and a carbamate (methomyl) with acetylcholinesterase (AChE).

by an acidic group (probably from aspartate) in what is called the anionic binding site. This binding of the choline to the anionic binding site is probably responsible for the initial complex formation between the acetylcholinesterase and acetylcholine. It is the serine hydroxyl group that attacks the carbonyl carbon of acetylcholine leading to acylation of the acetylcholinesterase and release of choline. The acyl group is then rapidly displaced from the serine hydroxyl group leading to a release of acetic acid and a regeneration of acetylcholinesterase. Inhibition of acetylcholine-sterase can, obviously, lead to a build up of acetylcholine at the post- synapse resulting in a total disruption of nerve function, and ultimately cause death.

The organophosphorus insecticides (Figure 6) are a large and diverse group of phosphoric acid esters which can be divided into two broad subclasses: the phosphates which are directly active against acetylcholinesterase and the phosphorothionates that require

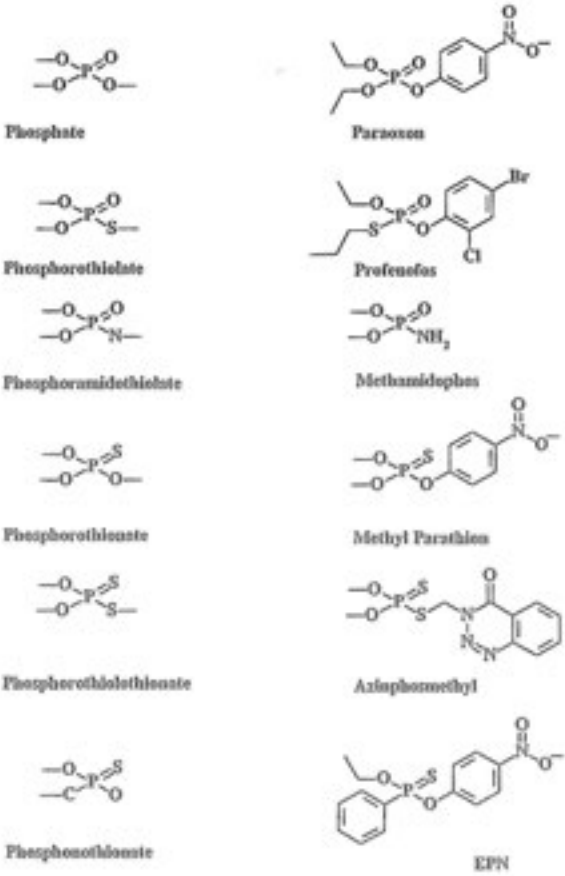


Figure 6. Examples of the different classes of organophosphorus insecticides.

activation in order to inhibit acetylcholinesterase (see section on metabolism). Included in the phosphate subclass are: the phosphates, dicrotophos (Bidrin®), monocrotophos (Azodrin®), naled (Dibrom®), paraoxon; the phosphorothiolates, profenofos (Curacron®); and the phosphoramidothiolates, acephate (Orthene®), methamidophos (Monitor®) (Figure 6, 14). In the phosphorothionate subclass are: the phosphorothionates, chlorpyriphos (Lorsban®, Dursban®), methyl parathion and parathion; the phosphorothiolothionates, azinphosmethyl (Guthion®), dimethoate (Cygon®), malathion, sulprofos (Bolstar®); and the phosphonothionates such as EPN (Figure 6, 14).

Organophosphorus insecticides act by binding with acetylcholinesterase (Matsumura, 1985). Unlike acetylcholine, when organophosphorus insecticides react with the serine hydroxyl group of the acetylcholinesterase active site, the reaction proceeds to the point where the serine hydroxyl is "phosphorylated" (Figure 5) but no further since the final steps in regeneration of the acetylcholinesterase (i.e. the reaction with water) occur only very slowly (Eto, 1974). Thus, phosphorylation of the acetylcholinesterase by organophosphorus insecticides effectively inhibits acetylcholinesterase resulting in an over stimulation of the post-synaptic nerve axon by the excess acetylcholine present.

For the organophosphorus insecticides, the process of phosphorylation is the critical step in determining the activity of a given compound (O'Brien, 1976). A primary factor influencing the efficacy of organophosphorus insecticides is the reactivity of the phosphorus atom to attack by the serine hydroxyl group. In the case of organophosphorus compounds such as paraoxon, and methyl paraoxon, this reactivity is influenced, in part, by the ability of substituents on the phenyl ring (the group that "leaves" when methyl paraoxon reacts with acetylcholinesterase; Figure 5) to make the phosphorus atom more reactive to the serine hydroxyl. Likewise, the size and composition of the alkyl groups also can influence that ability of the organophosphorus insecticide to fit into the esteratic active site. For example, in a series of *O*-alkyl *S*-(4-chlorophenyl) ethylphosphonothiolothinates and *O,O*-dialkyl *O*-(4-nitrophenyl) phosphorothionates, the topical toxicity to tobacco budworm larvae declined as the size of the alkyl group increased from methyl to ethyl to propyl (Wolfenbarger, 1972). There are several excellent reviews of these structure activity relationships (Eto, 1974; Fukuto, 1976, 1979; Magee, P. S., 1982; Fukuto and Keadtisuke, 1992).

CARBAMATES

Carbamates are esters consisting of an alcohol moiety such as naphthol, a substituted phenol, heterocyclic enol or an oxime, and a carbamic acid moiety, most commonly the *N*-methylcarbamic acid. Carbamates used on cotton include: the oxime carbamates, aldicarb (Temik®), methomyl (Lannate®, Nudrin®), thiodicarb (Larvin®), the phenyl carbamates, carbofuran (Furadan®); and the naphthyl carbamates, carbaryl (Sevin®) (Figures 7, 15). Like the organophosphorus insecticides, carbamates act to inhibit the acetycholinesterase of both insects and mammals. The mechanism of acetycholinesterase inhibition is very similar to that of the organophosphorus insecticides (Figure 5); however, there are significant differences between the

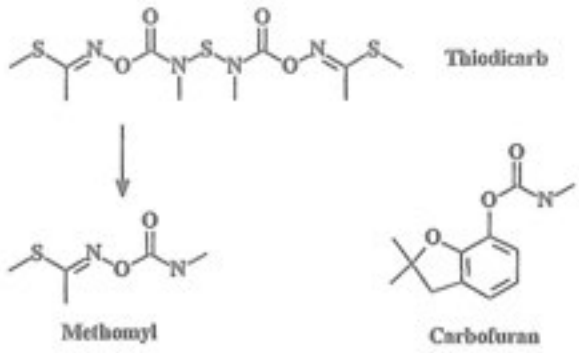


Figure 7. Structures of the carbamates carbofuran, methomyl and thiodicarb.

organophosphorus insecticides and the carbamates, especially relative to regeneration of acetylcholinesterase following inhibition and the structural requirements for activity.

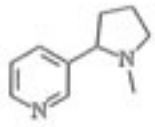
For the organophosphorus insecticides, regeneration of the inhibited acetylcholinesterase is exceedingly slow (several hours to days; Eto, 1974). On the other hand, regeneration of the carbamates is far more rapid (about 15 minutes). This relatively rapid rate of regeneration is virtually universal for all commercial carbamates since most are *N*-methyl carbamates resulting in the identical carbamylated enzyme. The structural requirements for good carbamate activity are also quite different from those necessary for the organophosphorus insecticides. The activity of the oxime carbamates such as aldicarb (Temik®) and methomyl (Lannate®, Nudrin®) appear to be related to their ability to mimic acetylcholine (Magee, T. A., 1982), while activity in the phenyl carbamates such as carbofuran (Furadan®) seems to be closely tied to the electron donating capacity of the substituents and steric requirements that affect ability to bind to one of several proposed binding sites (O'Brien, 1976). The necessity of these structural requirements is supported by kinetic studies of carbamates with acetylcholinesterase, which indicate that the formation of the carbamate-acetylcholinesterase complex is the critical step in the reaction. Very complete evaluations of carbamates structure-activity relationships are given by Fukuto (1976) and Goldblum *et al.* (1981).

Given the high mammalian toxicity of many carbamates such as aldicarb (Temik®), methomyl (Lannate®, Nudrin®), and carbofuran (Furadan®), a great deal of effort has gone into devising analogs, e.g., thiodicarb (Larvin®) (Figure 7) that upon metabolism by insects are converted back to the parent carbamate (e.g., methomyl). When metabolized by mammals, these compounds are converted to non-toxic products (Fukuto, 1984; Drabek and Neumann, 1985).

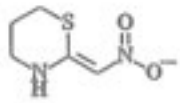
NITROMETHYLENES AND CHLORONICOTINYLS

As discussed above, the organophosphorus and carbamate insecticides disrupt nervous transmission by preventing the breakdown of the neurotransmitter acetylcholine.

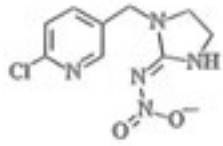
Other insecticides function by binding directly to the acetylcholine receptors to cause an over stimulation of the nervous system. Two classes of these receptors exist in insects and mammals; muscarinic and nicotinic (Matsumura, 1985). In insects the nicotinic receptors appear to predominate while in mammalian systems the predominate acetylcholine receptors appear to be muscarinic (Breer, 1985; Eldefrawi and Eldefrawi, 1990; Eto, 1992) suggesting that it may be a good site for the development of new insecticides (Eto, 1992). The insecticidal activity of nicotine (Figure 8) is well known (Eldefrawi, 1985; Matsumura, 1985) and its mode of action appears to involve binding to the nicotinic acetylcholine receptors, acting as an agonist at low concentrations and as an antagonist at higher concentrations (Eldefrawi, 1985). Although a variety of nicotinoids (synthetic nicotine analogs) have been isolated or synthesized (Eldefrawi and Eldefrawi, 1990) none have led to commercial products. The heterocyclic nitromethylenes (Figure 8) have been identified as acetylcholine agonists at the nicotinic receptor site (Eldefrawi and Eldefrawi, 1990) and some of these compounds have insecticidal activity (Soloway *et al.*, 1978). A hybrid between the nitromethylenes and nicotine is the nitroguanidine or chloronicotinyl insecticide, imidacloprid (Mullins, 1992; Moffat, 1993; Leicht, 1993; Figure 8). Imidacloprid is being developed for the control of sucking insects including aphids, thrips and whiteflies on cotton (Elbert *et al.* 1992; Mullins, 1992). Like nicotine, imidacloprid appears to act on the nicotinic receptor and appears to function as an acetylcholine agonist (Mullins, 1992). Insects resistant to organophosphates and carbamates were not resistant to imidacloprid (Mullins, 1992), an observation consistent with the differences in the respective modes of action.



Nicotine



Nitromethylene insecticide



Imidacloprid

Figure 8. Structures of nicotine, a nitromethylene insecticide and imidacloprid.

AVERMECTINS

An additional target for insecticides in the insect nervous system exists in the form of the peripheral nervous system. Unlike the central nervous system, which is generally agreed upon as using acetycholine as the synaptic stimulatory neurotransmitter, synaptic transmission in the peripheral nervous system of insects (at least at the neuromuscular junctions) is mediated by a stimulatory neurotransmitter, glutamic acid (Figure 4) and an inhibitory neurotransmitter, *gamma*-aminobutyric acid (Smyth, 1985; Shankland and Frazier, 1985) (Figure 4).

Abamectin (Affirm®, Zephyr®) (mixture of avermectin B_1a (Figure 9) and avermectin B_1b) is a microbiologically derived insecticide that acts on the insect nervous system (Fisher, 1990; 1993; Lasota and Dybas 1991). Although a number of target sites have been proposed, much of the evidence suggests that the avermectins interact with chloride channels (Turner and Schaeffer, 1989), and in particular *gamma*-aminobutyric acid gated chloride channels. The avermectins appear to open chloride channels acting as *gamma*-aminobutyric acid agonists at binding sites in the chloride channel, enhancing the action of *gamma*-aminobutyric acid at the receptor site or stimulating the presynaptic release of *gamma*- aminobutyric acid (Fisher, 1985; Miller and Chambers, 1987; Turner and Schaeffer, 1989). Although the structural requirements

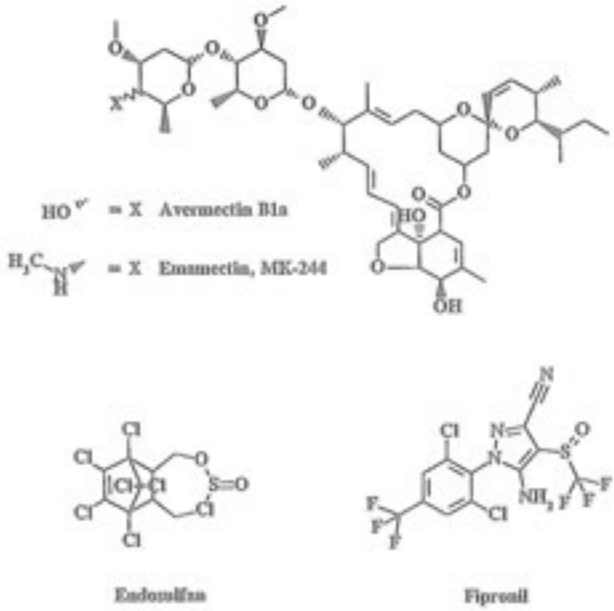


Figure 9. Structures of the avermectins, abamectin and emamectin (MK-244); the cyclodiene, endosulfan; and the phenylpyrazole, fipronil.

for insecticidal activity in the avermectins currently appears to be somewhat restrictive (Fisher, 1985; Fisher and Mrozik, 1989), undoubtedly improvements in avermectin chemistry will occur. These advances will lead to more potent analogs with better field residual and efficacy, as has been demonstrated by the development of the semi-synthetic avermectin analogs MK-243 and MK-244. Abamectin (Affirm®, Zephyr®) is a potent miticide, but is weak on insects such as the lepidoptera (Fisher, 1993). Avermectin derivatives that are more effective against lepidopterans have been a research focus for some time (Fisher, 1990, 1993), and some of the 4"-amino derivatives such as MK-243 (Dybas and Babu, 1988) and the 4"-epi-methylamino-4"-deoxyavermectin (emamectin, MK-244; Figure 9) appear to be much more effective against target lepidopterans than other derivatives of avermectin (Lasota and Dybas, 1991; Fisher, 1993). Topical bioassays of abamectin (Affirm®, Zephyr®) on the tobacco budworm show it to be as active as permethrin (Ambush®, Pounce®) (Table 2). Although there are currently no data available for cotton insect pest resistance to abamectin, information from studies using other insects is available. In some of these studies there was little cross-resistance to abamectin in insects resistant to cyclodiene, organophosphorus and pyrethroid insecticides (Roush and Wright, 1986; Cochran, 1990), while other studies found varying degrees of cross-resistance to abamectin in insects resistant to pyrethroids (Scott, 1989) or multiple insecticides (Abro *et al.*, 1988). Insect resistance to abamectin can result from an altered target site (Konno and Scott, 1991), reduced penetration (Konno and Scott, 1991) or enhanced metabolism (Argentine *et al.*, 1992). Available information suggests that the cross-resistance to abamectin is a function of enhanced metabolism, most likely due to monooxygenases (Abro *et al.*, 1988; Scott, 1989). Thus, while the avermectins are currently only used (in cotton) for mite control, they represent a class of chemistry that may become more important to cotton insect control as problems with resistance to the pyrethroids and other insecticides continue to increase (Campanhola and Plapp, 1987; Leonard *et al.*, 1987; Sparks *et al.*, 1993a).

CYCLODIENES

The cyclodienes are chlorinated insecticides resulting from a Diels-Alder reaction. Like DDT they were discovered during the late 1940s and early 1950s and have long since reached their zenith, falling increasingly into disuse. With the possible exception of endosulfan (Thiodan®) (Figure 9), most of the cyclodienes are highly persistent compounds. This persistence has contributed to the banning by EPA of most of the cycylodienes, and those that remain in the market are relatively little used.

The cyclodienes have for some time been viewed as acting to stimulate the release of acetycholine from the presynapse (Corbett *et al.*, 1984; Matsumura, 1985). Recent evidence, however, suggests that the cyclodienes may also be acting as *gamma*-aminobutyric acid (Figure 4) antagonists (Matsumura, 1985; Bloomquist *et al.*, 1987; Matsumura *et al.*, 1987), presumably at the picrotoxinin binding site of the chloride ionophore. Since *gamma*-aminobutyric acid may also function as an inhibitory neurotransmitter for chloride channels in the central nervous system of some insects

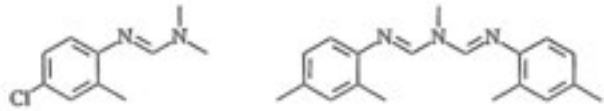
(Lummis *et al.*, 1987), as well as the neuromuscular junctions (Smyth, 1985), the *gamma*-aminobutyric acid antagonistic activity of the cyclodienes seems consistent with their apparent acetycholine stimulatory activity.

PHENYLPYRAZOLES

The phenylpyrazoles or fiproles are a new class of promising insecticides that act on the insect nervous system. Currently one member of this chemical family, fipronil (Figure 9), is under development as an insecticide with a wide spectrum of proposed uses including the control of the boll weevil and thrips in cotton (Colliot *et al.* 1992). Some phenylpyrazoles such as fipronil appear to act by blocking the *gamma*-aminobutyric acid gated chloride channel (Colliot *et al.* 1992; Cole *et al.* 1993; Moffat, 1993) in a manner similar to the cyclodienes. Studies indicate that these phenylpyrazoles are not cross-resistant with pyrethroid insecticides (Colliot *et al.* 1992),. However, studies also show that cyclodiene (e.g. dieldrin) resistant insects are cross-resistant to at least some of the phenylpyrazoles (Colliot *et al.* 1992; Cole *et al.* 1993), which is consistent with their mode of action.

FORMAMIDINES

Formamidine insecticides, such as chlordimeform (Fundal®, Galecron®) and amitraz (Ovasyn®) (Figure 10), act by affecting the insect nervous system, but not in the



Chlordimeform **Amitraz**

Figure 10. Structures of formamidines chlordimeform and amitraz

manner of the organophosphorus or carbamate insecticides. Available information suggests that the formamidines act as agonists of octopamine (Figure 4) (Hollingworth and Lund, 1982), a biogenic amine that functions as neuromodulator, neurohormone and neurotransmitter. Octopamine is, among other things, involved in the mobilization of carbohydrates and lipids, control of visceral muscles and insect behavior (Evans, 1985; Orchard and Lange, 1987). Extensive structure activity studies (Chang and Knowles, 1977; Knowles, 1982, 1987) support the octopamine agonist concept for insects in that formamidines that are most effective tend to resemble octopamine chemically (Hollingworth and Lund, 1982; Knowles, 1982).

As insecticides and acaricides, the formamidines are somewhat restricted in their spectrum of activity being limited to mites, ticks, lepidopterans and hemipterans (Hollingworth and Lund, 1982). Due, in part, to the rather exacting requirements for activity, commercial development of this class of insecticides has been rather limited.

Only two compounds have found wide commercial use, chlordimeform (Galecron®, Fundal®) and amitraz (Ovasyn®) (Figure 10). Chlordimeform was widely used as an ovicide for the tobacco budworm, but it has been withdrawn from the market. Chlordimeform and amitraz both appear to enhance insecticidal activity when co-applied with pyrethroids or other insecticides in the laboratory and in the field (Plapp, 1987; Campanhola and Plapp, 1987, 1988). This enhanced toxicity may be due, in part, to formamidine induced alterations in insect behavior resulting in increased contact with the pyrethroid or other insecticide (Treacy *et al.*, 1987; Sparks *et al.*, 1988, 1989, 1991), and/or alterations at the target site (Liu and Plapp, 1992).

SPINOSYNS

Spinosad (proposed common name) is a naturally occurring mixture of spinosyn A (A83543A) and D (A83543D) (Figure 11). The spinosyns are a new class of fermentation-derived tetracyclic macrolides (Kirst *et al.*, 1992) that act via the insect nervous system and are especially active against a variety of lepidopterous pests (Sparks *et al.*, 1995). Available information suggests that the mode of action is unique, and is not cross-resistant with the target sites for any other known insect control agents (Anonymous, 1994). Spinosyn A is very effective against the tobacco budworm with activity in topical bioassays in the range of pyrethroids such as permethrin (Table 2). Tests of spinosyn A and spinosad have shown them to be effective on a variety of insecticide resistant field and laboratory (including pyrethroid resistant) strains, with no evidence to date of cross-resistance, and to possess very favorable mammalian toxicity (Table 2) and environmental profiles (Sparks *et al.*, 1995). Given the expanding problems of insecticide resistance in cotton, spinosyns such as spinosad should find a great deal of utility in cotton IPM and resistance management programs.

PYRROLES

A majority of the insecticides in use for cotton insect control act via the nervous system. However, the disruption of metabolic processes can also provide the necessary efficacy to serve as a target for insect control agents. One such metabolic process is mitochondrial respiration. Part of this process involves mitochondrial electron transport whereby NADH is re-oxidized by transferring its electrons through a chain of carriers to oxygen. During the electron transfer process down the electron transport chain, energy is trapped and stored in the high energy bonds of ATP through the process of oxidative phosphorylation. If oxidative phosphorylation becomes disconnected, or uncoupled, from the electron transport process, the production of ATP will be disrupted ultimately leading to death. While the inhibition of the mitochondrial electron transport process (MET) is the basis for the insecticidal activity of rotenone (Fukami, 1985), and apparently several new acaricides (Motoba *et al.* 1992; Hollingworth *et al.*, 1994), the uncoupling of oxidative phosphorylation from MET is the basis for the action of insecticides and acaricides such as the dinitrophenols as well as others (see below).

The insecticidal pyrroles are an outgrowth of the discovery that a natural pyrrolomycin, dioxapyrrolomycin (Figure 11), isolated from a strain of *Streptomyces*

possessed insecticidal activity (Addor *et al.*, 1992; Kuhn *et al.*, 1993). Extensive structure activity studies around the pyrroles led to the discovery of AC 303,630 (Pirate®; Figure 11) (Addor *et al.*, 1992). AC 303,630 is a pro-insecticide that requires biological activation before it can act (Addor *et al.*, 1992; Kuhn *et al.*, 1993). Upon the metabolic removal of the *N*-ethoxymethyl group, the resulting pyrrole (Figure 11) functions as an uncoupler of oxidative phosphorylation (Addor *et al.*, 1992; Kuhn *et al.*, 1993; Moffat 1993). The pro-insecticidal nature of AC 303,630 also imparts a favorable mammalian toxicity profile (Kuhn *et al.*, 1993).

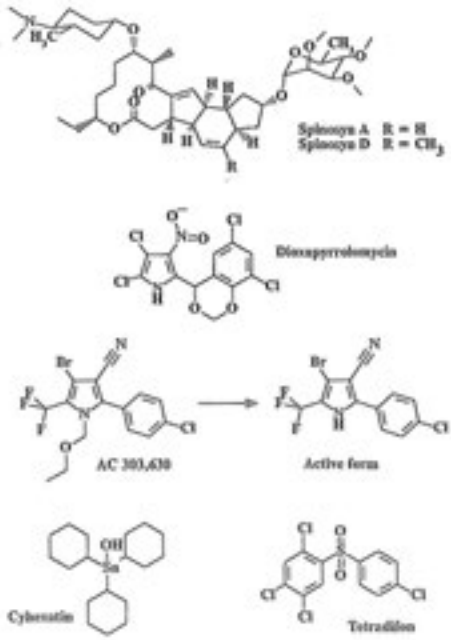


Figure 11. Structures of spinosyns A and D; the natural pyrrolomycin, dioxapyrrolomycin; the pyrrole, AC 303,630 and its bioactivation product; and two miticides, cyhexatin and tetradifon.

ORGANOTIN COMPOUNDS AND SULFUR CONTAINING ACARICIDES

The organotin compounds are exemplified by the miticide cyhexatin (Plictran®) (Figure 11), a tricyclohexylstannate derivative. Sulfur containing compounds such as tetradifon (Gardona®) (Figure 11) in which, typically, two benzene rings are attached to a sulfone, sulfonate or sulfide (Matsumura, 1985) comprise another group of miticides. Both the organotins and the sulfur- containing compounds appear to function as inhibitors of oxidative phosphorylation in mites (Desaiah *et al.*, 1973; Corbett *et al.*, 1984).

INSECT GROWTH REGULATORS

As a group of insecticides, the insect growth regulators (IGRs) encompass a diverse group of chemistries that act in some manner to disrupt insect growth and development (Hammock and Quistad, 1981; Retnakaran *et al.*, 1985; Sparks, 1990). Included in the IGRs are the juvenoids, diacylhydrazides and benzoylphenyl ureas.

Juvenoids — Juvenile hormone is a sesquiterpene epoxide (Figure 12) that is virtually unique to insects (Sparks 1990). Juvenile hormone works in concert with several other insect hormones and neurohormones, including the steroid hormone 20-hydroxyecdysone (Figure 12) and the neuropeptide, prothroacicotropic hormone, to regulate the molting process and, ultimately, insect metamorphosis. High levels of juvenile hormone maintain the larval or immature state while reduced levels of juvenile hormone initiate metamorphosis (Sparks, 1990). Juvenoids are compounds that mimic the action of juvenile hormone thereby disrupting the process of metamorphosis leading to a variety of deleterious effects (Staal, 1975; Hammock and Quistad, 1981; Sparks *et al.*, 1990). A great deal of effort has gone into the synthesis and testing of thousands of juvenoids (Slama *et al.*, 1974; Henrick 1982; Retnakaran *et al.*, 1985; Miyamoto *et al.*, 1993), some of which [epofenonane and fenoxycarb (Logic®)] (Figure 12) have been evaluated on the bollworm/tobacco budworm (Guerra *et al.*, 1973; Table 2) and the boll weevil (Moore, 1980). Although there currently are no juvenoids in wide use for cotton insect control, new compounds (eg. pyriproxyfen; Figure 12; Miyamoto *et al.*, 1993) and uses (eg. ovicide; Masner *et al.*, 1987) continue to be discovered. Thus, the juvenoids may yet find a role in cotton IPM.

Diacylhydrazides — The diacylhydrazides, a relatively recent and unique class of IGR (Hsu, 1991), are typified by RH 5992 (Figure 12). Although they do not yet have application to cotton insect control, some of these insecticides are effective against a variety of lepidopteran pests (Hsu, 1991; Heller *et al.*, 1992). In insects the molt that occurs at the end of each instar in larval or immature insects is initiated by 20-hydroxyecdysone (Figure 12). The available data suggest that the diacylhydrazides disrupt the molting process by functioning as ecdysone agonists (Wing, 1988; Wing *et al.*, 1988; Wing and Aller, 1990). For insects other than the Lepidoptera, a second non-endocrine mode of action may also be involved in the insecticidal activity observed for these nonsteroidal ecdysone agonists. Recent data suggest that the diacylhydrazides can also disrupt the insect nervous system by blocking potassium channels (Salgado, 1992).

Benzoylphenyl Ureas — Unlike the juvenoids and diacylhyrazides, the benzoylphenyl ureas have found a limited use for the control of cotton insect pests such as the boll weevil. The benzoylphenyl ureas are a rather novel class of insecticidal compounds that have their origins in a fortuitous accidental discovery by the scientists at Philips-Duphar in the early 1970s (Verloop and Ferrell, 1977). This discovery very rapidly led to the development of diflubenzuron (Dimilin®) (Figure 12). These insecticidal compounds act only on immature stages and only then during the molting

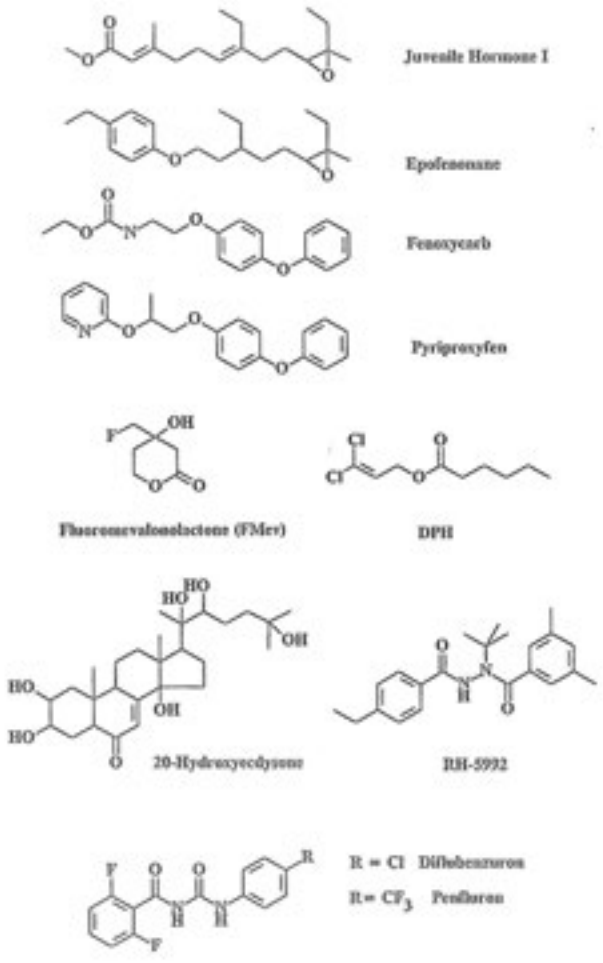


Figure 12. Structures of selected insect growth regulators (IGRs). Juvenile hormone I and the juvenoids, epofenonane, fenoxycarb and pyriproxyfen; the anti-juvenile hormones, FMev (fluoromevalonolactone) and DPH (3,3-dichloro- 2-propenyl hexanoate); 20-hydroxyecdysone (molting hormone) and a diacylhydrazide (non-steroidal ecdysone agonist), RH-5992; and the benzoylphenyl ureas, diflubenzuron and penfluron.

process. Unlike the most conventional insecticides, the benzoylphenyl ureas do not appear to affect the insect nervous system. Rather, chitin synthesis is inhibited leading

to a failure in the molting precess (Hajjar, 1985; Retnakaran *et al.*, 1985). Since chitin is lacking in plants and mammals, the benzoylphenyl ureas have an inherent selectivity over more conventional broad spectrum insecticides. While it is clear that the benzoylphenyl ureas act by inhibiting chitin synthesis, their exact mode of action is unclear. A number of mechanisms have been proposed for the benzoylphenyl ureas (Hajjar, 1985), including several centering on chitin synthetase, but none yet provide a completely satisfactory answer (Hajjar, 1985; Matsumura, 1985; Cohen, 1987, 1993; Grosscurt and Jongsma, 1987).

In spite of our ignorance concerning the exact mode of action for the benzoylphenyl ureas, a great deal of effort has gone into their development for control of cotton insect pests and other insect pests. A variety of insecticidally-active compounds have been developed (Retnakaran *et al.*, 1985). However, due to limited contact activity, benzoylphenyl ureas other than diflubenzuron (Dimilin®) have yet to find wide use in cotton insect pest control.

BACILLUS THURINGIENSIS Berliner

Bacillus thuringiensis Berliner var. *kurstaki* is a bacterium subspecies that produces a toxin that is toxic to lepidopterous larvae. Other subspecies are active against the Diptera (*Bacillus thuringiensis* var. *israelensis*) and Coleoptera. The toxic principle of *Bacillus thuringiensis* var. *kurstaki* is a crystalline *delta*-endotoxin (Bt toxin) which is activated by the high alkaline pH and proteolytic activity of the gut of lepidopterous larvae. The Bt toxin binds to specific receptors on the brush border membrane of midgut columnar cells (Gill *et al.*, 1992). Multiple receptors may be present, each binding a different group of Bt toxins (Yamamoto and Powell, 1993). The cells of the gut epithelium swell and then separate, disrupting the gut-hemocoele barrier (Luthy *et al.*, 1982; Roe *et al.*, 1985), leading to the death of the insect.

Although *Bacillus thuringiensis* has been available for the control of lepidopterous pests for some time, to varying degrees problems with production, environmental stability and efficacy relative to conventional insecticides have tended to limit their use (Gelernter, 1990; Gill *et al.*, 1992). However, advances in biotechnology have led to the insertion of genes for *Bacillus thuringiensis* toxins into a variety of plants, including cotton (Benedict *et al.*, 1992; Fischhoff, 1992; Periak and Fischhoff, 1993), and consequently this removes some of the problems associated with the use of *Bacillus thuringiensis* and its toxins. This transgenic Bt-cotton has the potential to provide good control of tobacco budworm and cotton bollworm larvae (Benedict *et al.*, 1992; Fischhoff, 1992), but should be used as part of a resistance management program to prevent the rapid selection of resistance to the *Bacillus thuringiensis* toxins (Gould,1991; Sparks *et al.*, 1993a; Whalon and McGaughey, 1993).

XENOBIOTIC METABOLISM

The following brief discussion of xenobiotic metabolism is meant to illustrate the presence and diversity of the metabolic capabilities present in cotton pest insects.

MONOOXYGENASES

Monooxygenases, also known as microsomal oxidases and mixed function oxidases, are involved in a variety of endogenous reactions including steroid and hormone synthesis, and fatty acid metabolism, all critical to the normal growth and development of insects (Wilkinson, 1985). The monooxygenases also are widely recognized as playing a major role in the metabolism of xenobiotics such as secondary plant compounds allowing the insect herbivores to survive on plants containing potentially toxic allelochemicals (Wilkinson, 1985). The monooxygenases are a family of membrane bound enzymes with broad and often overlapping substrate specificities (Wilkinson, 1983). Since the monooxygenases are particularly adept at dealing with lipophilic molecules and converting them to more polar compounds that can be more easily excreted, it is not surprising to find them playing a critical role in the general activation and catabolism of insecticides and in insect resistance to insecticides. The heart of the monooxygenase system is cytochrome P450 (Nakatsugawa and Morelli, 1976) which plays a critical role in substrate binding and insertion of an activated oxygen molecule into the substrate. The monooxygenases are involved in a number of reactions, all involving the insertion or addition of an oxygen into the substrate including aromatic and aliphatic hydroxylations, *O*, *S*, and *N*-dealkylation, *N*- and thioether oxidation, epoxidation, ester oxidation and desulfuration (Nakatsugawa and Morelli, 1976).

HYDROLASES

A variety of insecticides have ester linkages that are susceptible to hydrolysis by hydrolases that are typically in the extramicrosomal (soluble) fraction. Since both the pyrethroid and organophosphorus insecticides contain a variety of carboxyl, amide and phosphorus ester linkages, the hydrolases can be especially important in the metabolism of these two groups of insecticides. The hydrolases include the phosphotriesterases, carboxylesterases and carboxylamidases, which act on phosphorus triesters, carboxylesters and carboxylamide esters, respectively (Dauterman, 1976, 1985). A fourth group of hydrolases, the epoxide hydrolases, act on epoxide containing insecticides such as dieldrin, epofenonane, or in conjunction with the monooxygenases that epoxidize double bonds, converting the resulting epoxide to diols. Until recently the epoxide hydrolases were thought to be strictly membrane bound enzymes (Dauterman, 1985), however, epoxide hydrolases are now known to occur in the cytosolic fraction as well (Ota and Hammock, 1980).

GLUTATHIONE TRANSFERASES

The glutathione transferases are soluble enzymes that are important in the metabolism of organophosphorus insecticides (Dauterman, 1976, 1985). They require reduced glutathione as a co-factor. *O,O*-dimethyl organophosphorus insecticides are especially susceptible to attack by glutathione transferases leading to the *O*-dealkylation of the organophosphorus insecticide and the formation of an *S*-alkyl glutathione conjugate.

INSECTICIDE METABOLISM BY COTTON INSECTS

There have been numerous studies of insecticide metabolism by cotton insect pests (Table 3). However, for many of the currently used cotton insecticides detailed *in vivo* metabolism studies are lacking. The metabolism of many insecticides used for the control of bollworm/tobacco budworm has been reviewed (Bull *et al.*, 1987). In addition, there have been several extensive reviews of the metabolism of insecticides (Brooks, 1974; Eto, 1974; Kuhr and Dorough, 1976; Hammock and Quistad, 1981; Cool and Jankowski, 1985; Matsumura, 1985).

DDT AND PYRETHROID METABOLISM

As observed for many insects (Matsumura, 1985), DDT is metabolized to DDA by the tobacco budworm (Vinson and Brazzel, 1966) and to DDE via a glutathione-dependent DDT-dehydrochlorinase (Yang, 1976) in the tobacco budworm and bollworm (Gast, 1961; Vinson and Brazzel, 1966; Plapp, 1973).

Although the pyrethroid insecticides have been heavily used for insect control in cotton, information on the metabolism of these insecticides in bollworm/tobacco budworm or the boll weevil has been somewhat limited until recently. Permethrin (Ambush®, Pounce®) metabolism has been studied in the tobacco budworm and bollworm (Table 3) and, as has been observed in other studies (Soderlund *et al.*, 1983; Ruigt, 1985), permethrin is readily metabolized by ester hydrolysis (Figure 13, site 1) and aromatic and aliphatic hydroxylation (Figure 13, sites 2 and 3, respectively) (Bigley and Plapp, 1978; Nicholson and Miller, 1985). Permethrin was metabolized more rapidly by tobacco budworm larvae than bollworm larvae (Bigley and Plapp,

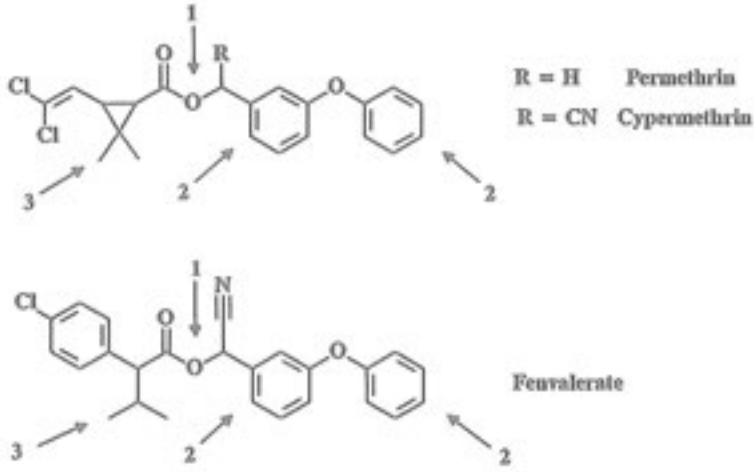


Figure 13. Examples of sites of metabolic attack for pyrethroids. Site 1 - ester hydrolysis. Site 2 - aromatic hydroxylation. Site 3 - aliphatic hydroxylation. All sites result in detoxification of the pyrethroids.

Table 3. Studies of insecticide penetration and metabolism in selected cotton insect pests.

Compound	*In vivo*	*In vitro*	Tobacco budworm	Boll-worm	Boll weevil	Twospotted spider mite	References
				DDT			
DDT	*			*			Gast, 1961
	*		*				Vinson and Brazzel, 1966
	*	*	*	*			Plapp, 1973
	*	*					Szeicz *et al.*, 1973
				PYRETHROIDS			
Permethrin	*		*	*			Bigley and Plapp, 1978
	*		*				Nicholson and Miller, 1985
	*		*				Payne, 1987
		*	*				Dowd and Sparks, 1987b
	*		*				Dowd *et al.*, 1987
	*	*	*				Sparks *et al.*, 1988
Cypermethrin	*		*				Lee *et al.*, 1989
	*		*				Little *et al.*, 1989
	*		*				Walker *et al.*, 1990
lambda-Cyhalothrin	*		*				Sparks *et al.*, 1988
Tralomethrin		*	*				Dowd and Sparks, 1988
Fenvalerate		*	*				Dowd and Sparks, 1987b
	*	*	*				Grissom *et al.*, 1989
Fluvalinate		*	*				Dowd and Sparks, 1988
Fenpropathrin	*	*					Dowd and Sparks, 1988
				ORGANOPHOSPHORUS INSECTICIDES			
Acephate	*		*		*		Bull, 1979
	*	*	*		*		Rose and Sparks, 1984
Chlorpyrifos	*	*	*				Whitten and Bull, 1974

Table 3. Continued.

Compound	*In vivo*	*In vitro*	Tobacco budworm	Boll-worm	Boll weevil	Twospotted spider mite	References
Chlorpyrifos-methyl	*	*	*				Whitten and Bull, 1974
Dicrotophos	*		*	*			Bull and Lindquist, 1964
Dimethoate	*		*	*			Bull *et al.*, 1963
Fenitrothion	*	*	*	*			Plapp, 1973
Malathion	*		*				Szeicz *et al.*, 1973
	*	*	*	*			Plapp, 1973
Mephosfolan	*		*				Hollingshaus *et al.*, 1984
Methyl parathion	*	*	*				Whitten and Bull, 1978
	*		*				Szeicz *et al.*, 1973
Mono-crotophos	*		*	*	*		Bull and Lindquist, 1966
Phosphamidon	*				*		Bull *et al.*, 1967b
Sulprofos	*		*		*		Bull, 1980
Trichlorfon	*		*				Bull and Ridgway, 1969
GC-6506-sulfone	*	*	*				Bull and Whitten, 1972
GS-13005	*		*				Bull, 1968
RH-0994	*		*		*		Bull *et al.*, 1983
				CARBAMATES			
Carbaryl	*			*	*		Andrawes and Dorough, 1967
	*	*	*	*			Plapp, 1973
	*		*				Szeicz *et al.*, 1973
Methomyl	*					*	Gayen and Knowles, 1981
Aldicarb	*		*		*		Bull *et al.*, 1967a
	*					*	Chang and Knowles, 1978

Table 3. Continued.

Compound	*In vivo*	*In vitro*	Tobacco budworm	Boll-worm	Boll weevil	Twospotted spider mite	References
				CYCLODIENES			
Aldrin	*	*	*				Bull and Whitten, 1972
	*	*	*	*			Plapp, 1973
	*		*				Whitten and Bull, 1978
Endrin	*		*				Szeicz *et al.*, 1973
	*		*				Polles and Vinson, 1972
				FORMAMIDINES			
Chlordimeform	*					*	Chang and Knowles, 1977
Amitraz	*		*	*			Knowles and Hamed, 1989
	*		*			*	Franklin and Knowles, 1984
	*		*				Sparks *et al.*, 1989
	*		*				Sparks *et al.*, 1993b
BTS-27271	*		*	*			Knowles and Hamed, 1989
				BENZOYLPHENYL UREAS			
Diflubenzuron	*				*		Still and Leopold, 1978
	*				*		Chang and Stokes, 1979
	*				*		Bull and Ivie, 1980
	*					*	Franklin and Knowles, 1981
Penfluron	*				*		Chang and Woods, 1979
				JUVENOIDS			
Fenoxycarb	*		*				Mauchamp *et al.*, 1989
				AVERMECTINS			
Abamectin	*		*	*			Bull, 1986

1978). The rate of ester hydrolysis is influenced by the steric configuration of the acid moiety and whether the alcohol moiety is a primary or secondary alcohol. The *trans* isomer of permethrin is much more readily hydrolyzed than is the more sterically hindered *cis* isomer (Bigley and Plapp, 1978; Dowd and Sparks, 1987a). The addition of a cyano group to the *alpha*-carbon of the 3- phenoxybenzyl alcohol moiety converts the primary alcohol of permethrin (Ambush®, Pounce®) into a secondary alcohol, cypermethrin (Ammo®, Cymbush®) (Figure 13), which is more difficult to hydrolyze (Soderlund *et al.*, 1983; Ruigt, 1985). Although not directly comparable, fenvalerate (Pydrin®), fluvalinate (Mavrik®) and tralomethrin (Scout®) all contain an *alpha*-cyano group in the alcohol and all are hydrolyzed *in vitro* at rates far below that of *trans*-permethrin in the tobacco budworm (Dowd and Sparks, 1988). The activity of the enzymes involved in the hydrolysis of both permethrin isomers and fenvalerate increases during the course of larval development (Dowd and Sparks, 1987b). Recent studies comparing the relative rates of permethrin versus *lambda*-cyhalothrin (Karate®) turnover found the latter to be much more resistant to metabolism (Sparks *et al.*, 1988). *Trans*-cypermethrin penetrated more slowly into pyrethroid-resistant tobacco budworm larvae than into pyrethroid- susceptible tobacco budworm larvae (Little *et al.*, 1988). The pyrethroid- resistant strain appeared to metabolize the *trans*-cypermethrin more rapidly than the susceptible strain. In both strains the 2'/4'-*trans*-cypermethrin and the dichlorovinyl acid from *trans*-cypermethrin were found to be present. This suggests the presence of both oxidative and hydrolytic pathways (Little *et al.*, 1988, 1989). Other studies support the presence of both pathways for cypermethrin (Ammo®, Cymbush®) metabolism (Lee *et al.*, 1989). Although there has been a study of fenvalerate penetration into larvae of the tobacco budworm (Grissom *et al.*, 1989), to date the *in vivo* metabolism of fenvalerate and several other pyrethroids registered for use on cotton including fluvalinate (Mavrik®), tralomethrin (Scout®), biphenthrin (Capture®) and cyfluthrinate (Baythroid®) has not been evaluated in either the bollworm/tobacco budworm or the boll weevil. Studies of fenvalerate (Pydrin®) metabolism in the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Soderlund *et al.*, 1987) and horn fly, *Haematobia irritans* (L.) (Bull *et al.*, 1988) indicate that oxidative pathways predominate.

METABOLISM OF ORGANOPHOSPHORUS INSECTICIDES

The organophosphorus insecticides are subject to a variety of metabolic modifications including monooxygenase based reactions: thiophosphate (P=S) to phosphate (P=O) conversion; *O*-dearylation; *O*- and *S*-dealkylation; *S*-alkyl oxidation; and *N*-dealkylation (Figure 14). The hydrolases in the form of phosphotriesterases (Figure 14, site 2), carboxylesterases (Figure 14, site 6) and carboxylamidases (Figure 14, site 7) are important, as are the glutathione *S*-transferases. These latter hydrolases also are important in the *O*- dealkylation of organophosphorus insecticide (Figure 14, site 3), especially where the alkyl groups are *O*-methyl.

The major metabolic pathways for most organophosphorus insecticides include cleavage of *O*- and *S*-aryl and alkyl phosphorus bonds by a combination of phospho-

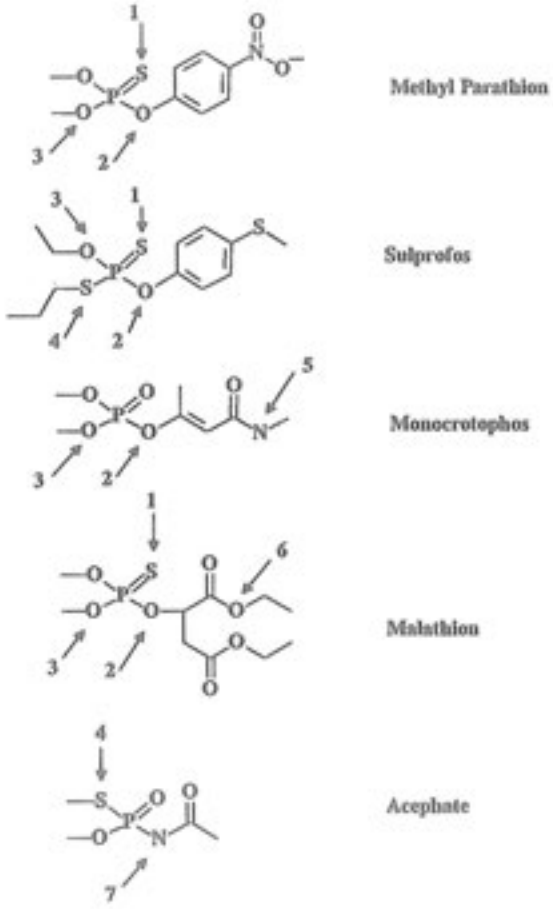


Figure 14. Examples of sites of metabolic attack for organophosphorus insecticides. Site 1 - Oxidative desulfuration (P=S to P=O), activation. Site 2 - phosphotriester hydrolysis and/or oxidative dealkylation or dearylation, detoxification. Site 3 - *O*-dealkylation via glutathione transferases or monooxygenases, detoxification. Site 4 - thio oxidation, activation. Site 5 - *N*-dealkylation, activation. Site 6 - carboxylester hydrolysis, detoxification. Site 7 - Carboxylamide hydrolysis, activation (in this particular case).

triesterases, glutathione *S*-transferases and monooxygenases (Figure 14, sites 2 and 3). For phosphorothionates (thiophosphates) such as methyl parathion, oxidative desulfuration (P=S to P=O) of the phosphorothionate to the oxon is also an important reaction (Figure 14). Typically *O*- and *S*- dealkylation and dearylation are detoxifying reactions, often followed by the rapid conjugation and excretion of the compound (Eto, 1974; Buchel, 1983). Likewise, organophosphorus insecticides such as malathion are also detoxified by carboxylesterases acting on carboxylester linkages (Figure 14, site 6). However, many reactions involving organophosphorus insecticides, including oxidative desulfuration, serve to activate or increase the toxicity of the parent organophosphorus insecticide.

Phosphates such as methamidophos (Monitor®), mevinphos (Phosdrin®), monocrotophos (Azodrin®), naled (Dibrom®) and profenofos (Curacron®) are all active as inhibitors of acetylcholinesterase, whereas phosphorothionates such as azinphos-methyl (Guthion®), chlorpyrifos (Lorsban®, Dursban®), EPN, malathion, methyl parathion, parathion and sulprofos (Bolstar®) all require metabolism (conversion) by monooxygenases to the corresponding phosphates (oxons) before they can effectively inhibit acetylcholinesterase. For example, parathion, malathion (Cythion®) and dimethoate (Cygon®) are 218, 750 and 5357 times less active towards house fly head acetylcholinesterase than their corresponding oxons (Eto, 1974). For many of the thiophosphate insecticides studied in the bollworm/tobacco budworm and the boll weevil, the oxon analogs of chlorpyrifos, chlorpyrifos methyl (Whitten and Bull, 1974), dimethoate (Bull *et al.*, 1963), methyl parathion (Whitten and Bull, 1978) and GS-13005 (Bull, 1968) have been identified as metabolites.

Sulfoxidation by monooxygenases of *S*-alkyl groups of organophosphorus insecticides (Figure 14, site 4) such as profenofos (Curacron®) and potentially sulprofos (Bolstar®) and RH-0994 can also result in increased toxicity (Wing *et al.*, 1982). *S*-alkyl sulfoxidation of methamidophos (Monitor®) has been used to explain the *in vivo* toxicity of an otherwise poor *in vitro* acetylcholinesterase inhibitor (Eto *et al.*, 1977; Magee, P. S., 1982), and the *S*-methyl has been identified as being the leaving group (Thompson and Fukuto, 1982). However, where the *S*-alkyl group is small (i.e. the *S*-methyl of methamidophos) sulfoxidation may not occur (Wing *et al.*, 1982), and may not be necessary to explain the biological activity of this insecticide (Khasawinah *et al.*, 1978; Magee, P. S., 1982; Rose and Sparks, 1984). Studies of sulprofos (Bull, 1980) in boll weevil and tobacco budworm found little in the way of metabolism, but since sulprofos requires biological activation for activity, these reactions were probably not detected due to the low specific activity of the compound used (Bull, 1980). Thioether sulfoxidation can also occur for *S*-alkyl or *S*-aryl substituents on the phenyl rings of organophosphorus insecticides such as sulprofos (Figure 14, site 4) resulting in increased reactivity with acetylcholinesterase (Eto, 1974; Bull, 1980; Bull *et al.*, 1976)

In addition to oxidative desulfuration and *S*-alkyl sulfoxidation, the *N*- dealkylation of organophosphorus insecticides such as monocrotophos (Azodrin®) to the unsubstituted amine also results in increased toxicity (Eto, 1974), but is only a minor pathway in the bollworm and boll weevil (Bull and Lindquist, 1966). The *N*-deacylation of

acephate (Orthene®) to methamidophos (Monitor®) (Figure 14, site 7) by carboxylamidases is also an activation reaction that readily occurs in the tobacco budworm (for which acephate is an effective insecticide) but not in the boll weevil (acephate is non toxic to the boll weevil) (Bull, 1979; Rose and Sparks, 1984).

METABOLISM OF CARBAMATES

Several carbamates have been and continue to be used for the control of cotton insect pests including carbaryl (Sevin®), carbofuran (Furadan®), methomyl (Lannate®, Nudrin®), aldicarb (Temik®), and thiodicarb (Larvin®). Carbamates are primarily metabolized by oxidative reactions and, to varying degrees, by ester hydrolysis (Figure 15) (Kuhr and Dorough, 1976). In the case of carbaryl metabolism by adult boll weevils and bollworm larvae, the hydrolysis product, 1-naphthol, accounted for 5.8 percent and 17.4 percent, respectively, of the applied dose 12 hours posttreatment (Andrawes and Dorough, 1967). However, it is likely that the 1-naphthol originated from the breakdown of an oxidation product, the *N*-hydroxylated carbaryl (Andrawes and Dorough, 1967). The other major metabolite in boll weevils and bollworms was the 5,6-diol of carbaryl, resulting from aryl hydroxylation by monooxygenases. Tobacco budworm larvae metabolize carbaryl faster than do larvae of the bollworm (Plapp, 1973).

As with carbaryl, the principle metabolites of aldicarb (Temik®) are the result of monooxygenase activity and include the *N*-hydroxy-aldicarb, the sulfoxide and the sulfone (Figure 15, site 4). Aldicarb is much more readily absorbed by the boll weevil than by the tobacco budworm (Bull *et al*., 1967a). As with the organophosphorus insecticides,

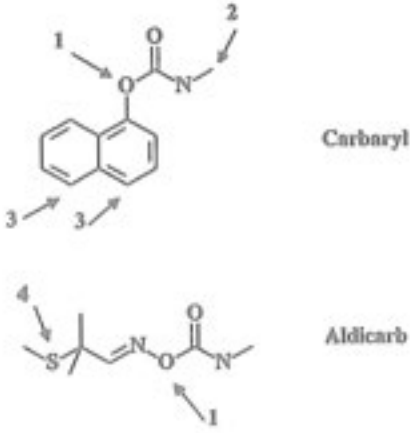


Figure 15. Examples of sites of metabolic attack for carbamate insecticides. Site 1 - carboxylester hydrolysis, detoxification. Site 2 - *N*-alkyl hydroxylation, detoxification. Site 3 - aromatic hydroxylation, detoxification. Site 4 - thioether oxidation, activation.

thioether oxidation to the sulfoxide is an activation reaction for aldicarb and is the predominant reaction for both the boll weevil, tobacco budworm, and twospotted spider mites (Bull *et al*., 1967a; Chang and Knowles, 1978). The oxidative *N*- demethylation of aldicarb appears to be a very minor pathway for the boll weevil and tobacco budworm. The recovery of oxime sulfoxide and sulfone indicates that hydrolysis of the aldicarb sulfoxide and sulfone occurs to some extent for the boll weevil, tobacco budworm (Bull *et al*., 1967a) and twospotted spider mite (Chang and Knowles, 1978). In part, the poor toxicity of aldicarb to tobacco budworm larvae versus the boll weevil appears to be due to differences in the sensitivity of their respective acetylcholinesterases (Bull *et al*., 1967a).

Although methomyl (Lannate®, Nudrin®), carbofuran (Furadan®) and thiodicarb (Larvin®) are also registered for the control of bollworm/tobacco budworm and the boll weevil, there appears to have been no studies of their metabolism in these insects. Based on studies with cabbage loopers (Kuhr, 1973), methomyl does not appear to form the sulfoxides and sulfones observed for aldicarb (Temik®). Rather it seems to decompose to form acetonitrile and carbon dioxide (Kuhr, 1973; Kuhr and Dorough, 1976). When the metabolism of methomyl was studied in the twospotted spider mite (Gayen and Knowles, 1981), methomyl oxime, several unidentified metabolites, and labeled CO_2 were detected. Studies of carbofuran metabolism in insects such as the saltmarsh caterpillar indicate that it is readily metabolized via monooxygenases to form 3-hydroxy carbofuran and its 3-keto analog, as well as the *N*-hydroxymethyl analog (Kuhr and Dorough, 1976).

METABOLISM OF CYCLODIENES

Endosulfan (Thiodan®) remains the only cyclodiene that is recommended for use in the control of bollworm/tobacco budworm on cotton in the United States. Although there are no reports of the metabolism of endosulfan in the bollworm/tobacco budworm or the boll weevil, its metabolism has been studied in other insects (Barnes and Ware, 1965; Brooks, 1974). Compared to other cyclodienes endosulfan is highly biodegradable (Brooks, 1974). The primary metabolite in insects occurs through oxidation of the sulfite moiety to the sulfate (Barnes and Ware, 1965; Brooks, 1974).

The metabolism of endrin has been studied in the tobacco budworm where the primary metabolites were tentatively identified as endrin-aldehyde and endrin-ketone (Polles and Vinson, 1972). Aldrin is more rapidly metabolized in the tobacco budworm than in the bollworm with dieldrin being the primary metabolite for both species (Plapp, 1973).

METABOLISM OF FORMAMIDINES

Metabolism studies of chlordimeform (Fundal®, Galecron®) in the twospotted spider mite indicate that chlordimeform is rapidly taken up and *N*-demethylated to the demethylchlordimeform followed by further *N*-demethylation to didemethylchlordimeform, the 4'-chloro-o-formotoluidide and 4'-chloro-o- toluidine (Figure 16) (Chang and Knowles, 1977). This pattern of metabolism is consistent with the formation of the more toxic *N*-demethychlordimeform (Chang and Knowles, 1977) and chlordimeform functioning as an octopamine agonist. Twospotted spider mite metabolism of amitraz (Ovasyn®) produced several metabolites including BTS-27271 (*N*'-(2,4-dimethyl-

phenyl)-*N*-methylformamidine; NOR-AM 49844), 2,4-dimethylformanilide and 2,4-dimethylaniline (Franklin and Knowles, 1984). As observed for chlordimeform, a metabolite (BTS-27271) may be responsible for the biological activity of amitraz (Franklin and Knowles, 1984; Knowles, 1987).

The metabolism of amitraz has also recently been examined in larvae of the tobacco budworm and bollworm (Knowles and Hamed, 1989; Sparks *et al.*, 1989). As observed for the spider mites, amitraz is converted to BTS-27271 (Knowles and Hamed, 1989; Sparks *et al.*, 1989), and other metabolites; 2,4- dimethylformanilide, 2,4-dimethylaniline and polar metabolites (Knowles and Hamed, 1989). Although higher titers of BTS-27271 were found in larvae of the bollworm when compared to larvae of the tobacco budworm (Knowles and Hamed, 1989), there were no differences in the titers of amitraz and BTS-27271 in pyrethroid susceptible and resistant larvae of the tobacco budworm (Sparks *et al.*, 1989). The metabolism of BTS-27271 by larvae of the bollworm and tobacco budworm also proceeded through the 2,4-dimethylformanilide, but not the 2,4- dimethylaniline (Knowles and Hamed, 1989). Eggs of the tobacco budworm also have the capability of converting amitraz to BTS-27271, which may be associated with its ovicidal activity (Sparks *et al.*, 1990, 1993b).

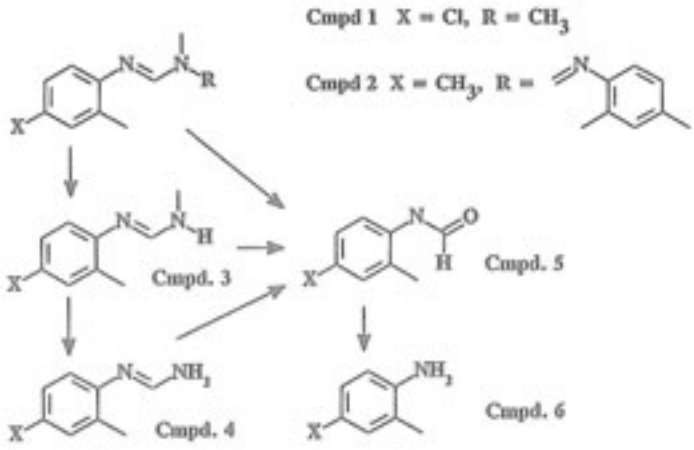


Figure 16. Examples of some of the metabolic pathways for the formamidines chlordimeform (1) and amitraz (2). Compound 3: demethylchlordimeform (X-C1); BTS-27271 (X-CH_3). Didemethylchlordimeform (4). Compounds 5 and 6 are metabolites for both chlordimeform (X-Cl) and amitraz (X-CH_3). [Information adapted from Chang and Knowles (1977), and Knowles and Hamed (1989).]

METABOLISM OF BENZOYLPHENYL UREAS

The metabolism of the benzoylphenyl ureas has been extensively studied in a variety of insects (Hammock and Quistad, 1981; Sparks and Hammock, 1983; Retnakaran *et al.*,

1985) including the boll weevil. The first studies of diflubenzuron (Dimilin®) metabolism in the boll weevil found only unchanged diflubenzuron internally and in the frass (Still and Leopold, 1978). Subsequent studies (Chang and Stokes, 1979) also found only unchanged diflubenzuron internally, but in the frass observed several conjugates of diflubenzuron hydroxylated in the 2 position of the chloroaniline ring or the 3 position of the difluorobenzamide ring. A further study of diflubenzuron metabolism in the boll weevil (Bull and Ivie, 1980) also found that diflubenzuron accounted for most of the internal radioactivity, but that small amounts of metabolites were produced and evidence suggested both conjugation and hydrolysis reactions. As with diflubenzuron, studies of penfluron (Figure 12) metabolism in the boll weevil found unchanged penfluron to account for virtually all of the internal radioactivity (Chang and Woods, 1979). Likewise metabolism of diflubenzuron by twospotted spider mites also proceeds very slowly, with unchanged diflubenzuron accounting for most of the radioactivity (Franklin and Knowles, 1981). However, major metabolites (5.8 to 7.7 percent of recovered radioactivity) appeared to be the result of hydrolysis while hydroxylation products of the chloroaniline ring were relatively minor (0.8 to 1.4 percent of recovered radioactivity) products.

METABOLISM OF JUVENOIDS

Although the metabolism of the insect juvenile hormones and juvenoids have received quite a bit of attention (Hammock and Quistad, 1981; Sparks and Hammock, 1983; Hammock, 1985; Retnakaran *et al.*, 1985), information concerning juvenoid metabolism in pests of cotton is very limited. The metabolism of the juvenoid fenoxycarb (Logic®) has been examined in fourth and fifth instar larvae of the tobacco budworm (Mauchamp *et al.*, 1989). While ester hydrolysis does not appear to be an important metabolic pathway, cleavage of the amide linkage and aromatic hydroxylation did appear to occur (Mauchamp *et al.*, 1989).

METABOLISM OF AVERMECTINS

Although there are numerous studies of ivermectin in mammals (Chiu and Lu, 1989) there is limited information on abamectin (Affirm®, Zephyr®) metabolism in insects. Avermectin B_1a was metabolized faster in bollworm larvae than in larvae of the tobacco budworm, and more accumulated in the heads of tobacco budworm larvae than in bollworm larvae (Bull, 1986); however, specific metabolites of avermectin were not identified. Studies with abamectin susceptible and resistant Colorado potato beetles suggest that oxidative metabolism predominates in insects, the major metabolite being the 3"-desmethyl avermectin B_1a, followed by the 24-hydroxy avermectin B_1a (Argentine *et al.*, 1992; Clark *et al.*, 1992).

SYNERGISM

In the control of cotton insect pests a common practice has been, and continues to be, the mixing of insecticides to either control several different pests with one application, or to increase the activity of a particular insecticide. In the broadest sense, synergism is

the enhancement of biological activity (usually toxicity) over and above that which would normally be expected from the separate components alone. In terms of cotton insect/mite control, synergism can occur when two or more insecticides and/or acaricides are mixed as in the case of toxaphene plus DDT, or when an insecticide and an insecticide synergist, such as piperonyl butoxide, are used together. In many cases, the resulting synergism is due to the detoxification of one component (insecticide) being blocked by another component (another insecticide or an insecticide synergist) (Wilkinson, 1976b). Piperonyl butoxide is commonly used as an insecticide synergist since it is an effective inhibitor of the monooxygenases involved in insecticide detoxification (Wilkinson, 1976b). Likewise, many organophosphorus insecticides are effective inhibitors of the hydrolases involved in the detoxification of pyrethroids and other organophosphorus insecticides (Eto, 1974; Soderlund *et al.*, 1983; Dowd and Sparks, 1987c). For example, the organophosphorus insecticide profenofos (Curacon®) is an effective inhibitor of the esterases responsible for the hydrolysis of pyrethroids (Soderlund *et al.*, 1983; Dowd and Sparks, 1987c). Mixing profenofos with permethrin (Ambush®, Pounce®) increases the topical toxicity of permethrin to larvae of the tobacco budworm by over four-fold (Dowd and Sparks, 1987; Dowd *et al.*, 1987).

Although inhibition of detoxification is one mechanism by which a synergist can function, other possibilities also exist. In recent years chlordimeform (Fundal®, Galecron®) has been found to synergize a variety of insecticides, including the pyrethroids (Plapp, 1976; El-Sayed and Knowles, 1984a,b; Campanhola and Plapp, 1987). It has been suggested that chlordimeform functions by increasing the binding of the pyrethroid at the target site (Chang and Plapp, 1983; Liu and Plapp, 1992). Another potential explanation lies in the octopamine agonist action of chlordimeform (Table 1), resulting in increased motor activity in the insects. Recent studies demonstrate that in contact bioassays, chlordimeform increases the uptake of radiolabeled permethrin or *lambda*-cyhalothrin by tobacco budworm larvae (Sparks *et al.*, 1988, 1989, 1991). Thus, in part, insecticide synergism by chlordimeform may result from increased insecticide contact on the part of chlordimeform-treated insects.

THE FUTURE AND NEEDS

For many cotton growing regions of the United States the pyrethroids currently provide effective control of the tobacco budworm - bollworm complex. However, pyrethroid resistance has become an increasingly important problem for cotton growers in parts of Louisiana, Mississippi and Texas (Sparks *et al.*, 1993a), just as it had for *Helicoverpa armigera* Hübner on cotton in Australia (Daly, 1988; Cox and Forrester, 1992), the horn fly, *Haematobia irritans* (Linnaeus) (Byford and Sparks, 1987), and the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Georghiou, 1986). Although alternatives to the pyrethroids exist in the form of some of the newer organophosphorus and carbamate insecticides, as well as others, these compounds are typically not as active as the pyrethroids and are generally more expensive. In addition, available data now suggest that there may also be resistance to some of these

organophosphorus and carbamate insecticides, possibly endosulfan, as well as the pyrethroids (Martin *et al.*, 1992; Elzen *et al.*, 1993; Kanga *et al.*, 1993; Sparks *et al.*, 1993a). Thus, it has become imperative to expand the search for new insecticides, and at the same time implement programs to preserve available compounds. In many cases, they represent a non-renewable resource (Hammock and Soderlund, 1986). Unfortunately, the cost of discovery for new replacement insecticides is an increasingly expensive process (Georghiou, 1986; Hammock and Soderlund, 1986) with the percentage of compounds making it to market steadily declining. However, there is some new chemistry on the horizon that may be available in the near future to potentially fill in any holes created by the loss of one or more of the currently available insecticides. The pyrrole AC 303,630 (Pirate®) and the avermectin analog emamectin (MK-244) represent two new chemistries that appear to have potential as insecticides for tobacco budworm larvae (Addor *et al.*, 1992; Kuhn *et al.*, 1993; Fisher, 1993; see also above). In addition, insecticides suitable for use against the tobacco budworm and other cotton pests may eventually come out research into the phenylpyrazoles (Colliot *et al.*, 1992), or the diacylhydrazides (Hsu, 1991; Heller *et al.*, 1992).

An important consideration with all of these materials is that a new mode of action does not necessarily mean there will be no cross-resistance from older insecticides to the new insecticide. For example, dimethoate (an organophosphate inhibitor of acetylcholinesterase) resistant house flies were found to be cross-resistant to methoprene, a juvenoid (juvenile hormone mimic) IGR (Hammock *et al.*, 1977). The basis for the dimethoate resistance, and the cross-resistance to methoprene, was an enhanced monooxygenase activity that could effectively metabolize both types of chemistries (Hammock *et al.*, 1977, Sparks and Hammock, 1983). Therefore, new chemistry or new modes of action can be useful tools in resistance management programs only if the resistance mechanisms (which may or may not be based on mode of action) do not overlap for the different insecticides involved. Conversely, compounds with the same mode of action do not necessarily have to be cross-resistant, especially if the resistance mechanism does not involve the insecticide target.

In addition to the chemistries mentioned, other leads for the development of new insecticide/acaricides are needed if we are to insure the future of cotton insect control. While there are a variety of methods available for achieving insecticide/acaricide selectivity and safety (Hollingworth, 1976; Drabek and Neumann, 1985), attacking a target unique to insects is conceptually the most appealing. In this respect the insect endocrine system appears to have some advantages for the development of safer insecticides/acaricides since, in several aspects, it appears to be unique to insects (Sparks, 1990). As already mentioned neither the juvenoids nor the diacylhydrazides have yet to find widespread use in cotton insect/mite control. However, these compounds aptly demonstrate that safe and selective insecticides/acaricides based on the insect endocrine system can be developed. Other approaches to exploiting the insect endocrine system for insect control include the development of anti-juvenile hormones that would affect the early larval development of pest lepidopterans. Given the chemical variety and numerous modes of action for the anti-juvenile hormones that have been identified (Staal, 1986;

Sparks, 1990) antagonism of juvenile hormone biosynthesis or action may yet yield useful insecticides. Indeed, for pest insects such as the tobacco budworm, some of the more recent anti-juvenile hormones (e.g. DPH, Table 2) are as active as some organophosphorus and carbamate insecticides (Quistad *et al.*, 1985).

Available information clearly demonstrates that an appreciation of the basic biochemistry and physiology of insects can be critical in the development of new insecticides. This concept is exemplified in the possibilities now being raised by the isolation, characterization and sequencing of insect neurohormones and neurotransmitters (Sparks, 1990; Masler *et al.*, 1993). These bioactive molecules present a host of new models for the production of synthetic analogs to be used as insecticides. Likewise, the incorporation of the genes for some of these neurohormones into plants or bacterial or viral vectors, presents new opportunities and new approaches for controlling insect pests (Hammock *et al.*, 1993).

However, to take advantage of these new approaches in insect/mite control, more information is needed on the basic insect/mite biochemistry and physiology, as well as on the mode of action of new and existing insecticides. Moreover, insects such as the tobacco budworm, bollworm and pink bollworm should be included as test animals. Some of this information can come from screening programs that have used cotton insect pests such as the tobacco budworm or bollworm in structure optimization studies (Soloway *et al.*, 1979; Henrick *et al.*, 1980; Plummer, 1984; Kuhn *et al.*, 1993), thereby making available very useful information on structure-activity relationships. Unfortunately, such information is typically not made available.

In addition to the search for new chemistry, the many resistance management programs instituted (Anonymous, 1986; Plapp, 1987) throughout the cotton growing areas of the United States hopefully will slow the rate at which pyrethroid resistance is developing (Graves *et al.*, 1988; Sparks *et al.*, 1993a). With programs such as these, the pyrethroids and other insecticides may yet remain useful in cotton insect pest management programs to provide the time needed to develop new and improve upon existing, cotton insect/mite control measures.

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Chapter 9

RESISTANCE TO PESTICIDES: MECHANISMS, DEVELOPMENT AND MANAGEMENT

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INTRODUCTION

Growers have been aware of resistance to insecticides in cotton pests for many years. They have come to expect that, given a chronic or endemic pest population, a new insecticide or acaricide has a certain life in the field before pest tolerance increases to unacceptable levels (Ivy and Scales, 1954; Brazzel, 1963; Bottrell and Adkisson, 1977; Sparks, 1981; Wood, 1981; Mani, 1990). It is only recently that resistance has become recognized by the industry as being manageable (LaFarge, 1985).

Resistance to insecticides and the related phenomena of pest resurgence and secondary pest outbreaks are said to be predictable from elementary theories of evolution and population dynamics (Berryman, 1991). It is impossible to spray any crop with a full rate dose of any modern residual neurotoxic insecticide without that dose eventually becoming a selecting dose. This is because, through time, the foliar applied dose degrades, usually slowly over a matter of days, from a killing dose to a selecting dose.

Agrochemical realities are driven by a need to produce only broad spectrum insecticides with a long residual activity for major markets like the cotton pest complex (Voss and Neumann, 1992). These characteristics also are ideal for the development of resistance, particularly the residual property (Denholm *et al.*, 1983; ffrench-Constant *et al.*, 1988a,b). Most other candidate insecticides, particularly selective insecticides that would fit ideally into insect pest management programs, are not developed because the return would not pay for the investment.

It is the selecting dose that leads to resistance problems. The natural play of a wide diversity of fitness and other genetic factors combined with high rates of reproduction, drive the response of pest populations toward ever greater tolerance so long as insecticides are being used frequently on a wide scale. These events rarely occur quickly. Instead, resistance gradually "creeps" into the agroeconomic mileu as resistance builds and declines in repeated cycles. This "ratchet up" effect of the alternate build up and decline of resistance to pyrethroid insecticides was seen each season in *Helicoverpa armigera* (Hübner) in Australia (Roush and Daly, 1990) and the same effect was

noticed in resistance monitoring data from tobacco budworm, *Heliothis virscens* (F.) in the United States Cotton Belt (Mullins *et al.*, 1991).

The "classic" signs of resistance are said to be increasing dose rates and decreasing treatment intervals. The onset of resistance is usually measured in years rather than months. In most cases resistance problems are caused in species that tend to be more endemic, because they would be under more constant selective pressure; however, the presence of resistance in pest insects, while almost always suspected, is proven only with a substantial amount of work.

The following quote from Professor Thomas F. Leigh (Personal communication) of the University of California, Davis is pertinent: "We presume there is resistance to several insecticides in our populations of aphid, bollworm [*Helicoverpa zea* (Boddie)], beet armyworm [*Spodoptera exigua* (Hübner)], cabbage looper [*Trichoplusia ni* (Hübner)], saltmarsh caterpillar [*Estigmene acrea* (Drury)] and a number of other pests. However, we have not conducted confirming tests that would verify resistance. While control failures that have occurred frequently could be related to application or weather, we are confident that many failures today relate to the selective pressure of the insecticides that used to be effective."

Dr. Leigh was referring to the pest-cotton complex in the Central Valley of California, but the same remarks with a slightly different range of pests could be true of any part of the Cotton Belt. Representatives from agrochemical industry spend a certain amount of their time verifying rumors of possible resistance (Davies, 1984). Gossip can have a profound influence on the widespread confidence that growers have in a particular pest control product.

REGIONAL PESTS AND RESISTANCE POTENTIAL

Although it is not the purpose of this chapter to document the presence of pest insects, the potential of insect pests to develop resistance is tied closely to species that visit the cotton fields each season. With a few outstanding exceptions like the boll weevil, *Anthonomus grandis grandis* (Boheman), the species that are more endemic and are treated more routinely with insecticides would be expected to develop resistance more readily.

Unfortunately for everyone, the mix of pest species changes every year, sometimes drastically, making predictions about pest pressure virtually impossible. The same impossibility of prediction holds true for gauging the chances of developing resistance, especially over a cotton growing area that extends from California to Virginia. Nevertheless, the insect pressure reported for 1991 (Head, 1992) is instructive and useful as a starting point (Table 1).

Comparing the percent yield reduction due to insect pests from 1989 to 1992 (Table 2), and ranking the pests in terms of causing the greatest damage, boll weevils were the worst pests in 1989, then the bollworm, and tobacco budworm complex caused the greatest losses in 1990 and 1992, while aphids caused the worst losses in 1991.

By comparing the five worst pests in terms of yield reduction across the Cotton Belt, aphids were fifth in 1989 with 0.55 percent yield reduction, 0.64 percent in 1990 and

Table 1. Cotton insect losses in the United States reported for 1991 growing season. (From Head, 1992.)[1]

Pests	Acreage infested	Number of insecticide applications[2]	Yield reduction	Bales lost
	(1,000 acres)		(%)	(1,000 bales)
Boll weevil	6,122	0.7	0.81	146.00
Bollworm/tobacco budworm	11,340	1.6	1.68	300.00
Fleahoppers	4,534	0.2	0.13	23.60
Lygus bugs	5,109	0.4	0.47	85.00
Leaf perforator	315	0.0	0.00	0.39
Pink bollworm	512	0.1	0.08	15.00
Spider mites	1,816	0.1	0.08	14.40
Thrips	7,035	0.3	0.13	22.50
Beet armyworm	2,305	0.1	0.02	3.66
Fall armyworm	1,805	0.0	0.03	5.03
Minor pests	3,018	0.1	0.08	13.80
Aphids	10,067	0.9	2.01	360.00
New pests	1,584	0.1	0.11	19.40
Western flower thrips	2,339	0.0	0.00	0.11

[1]Total acres harvested was 13,022,000; average yield was 1.38 bales/acre.
[2]Per acre for infested acreage.

they were the worst pest in 1991 with a yield reduction of 2.01 percent, and in 1992 dropped off the five worst list to be replaced by the sweetpotato whitefly, *Bemisia tabaci* (Gennadius). Over the same four years, lygus bugs as pests went from second and 2.05 percent yield reduction to 0.47 percent and fourth worst pest.

Table 2. Annual yield reduction of total United States cotton production ranked by top insect pests for the period 1989-1992. (From Head, 1990, 1991, 1992, 1993.)

Rank	1989		1990		1991		1992	
	Pest	Yield reduction	Pest	Yield reduction	Pest	Yield reduction	Pest	Yield reduction
		(%)		(%)		(%		(%)
1.	Boll Weevil	2.75	Bollworm	1.73	Aphid	2.01	Bollworm	2.2
2.	Lygus	2.05	Mites	1.24	Bollworm	1.68	Boll weevil	2.1
3.	Bollworm	1.87	Lygus	0.91	Boll weevil	0.81	Lygus	0.8
4.	Mites	1.11	Aphid	0.64	Lygus	0.47	Whitefly	0.5
5.	Aphid	0.55	Boll weevil	0.60	Leafhopper	0.13	Thrips	0.3

One would expect from this type of exercise that the insects listed in these tables are the prime candidates for the development of resistance. Indeed, research funding aimed at studies of insecticide resistance tends to be driven more by the magnitude and immediacy of current pest problems fueled by grower concerns, than by any rational, stable, longer-term approach.

For example, spider mites caused 1.11 percent yield reduction in 1989 and 1.24 percent yield reduction in 1990; however, in 1991 mites were credited with causing a 0.08 percent yield reduction and in 1992 a 0.2 percent reduction. Not only did they fall off of the worst five list, interest and support for resistance management waned. Thus, like cotton pests in general, insecticide resistance problems are a dynamic target.

An even more revealing statistic on these tables is the number of insecticide applications (Table 1). Costs are related to the number of applications. They also reflect the insecticide sales market. Older compounds like methyl parathion and malathion, long out of patent, would tend to be lower in cost. Insecticides like the pyrethroids would tend to be less expensive because several pyrethroid products are now competing for a cotton pest control market, that reportedly is worth US$ 300 million a year in the United States (Anonymous, 1990b).

If one is allowed to make risky conclusions based on these figures alone, one might be tempted to suspect that those cotton pest insects that are more endemic (show up on the five worst insect list every year) and show higher per application costs would be those insects that pose the greatest insecticide resistance problems. This is only partially correct because resistance can occur in smaller populations of regional pests that are not at the top of these lists (see, for example, the entries in Table 1 for "minor pests" and "new pests").

In 1991, aphids became significant cotton pests and were said to be responsible for the greatest losses attributed to one pest. If one follows the gradual increase in the severity of cotton pest control problems with aphids, a steadily increasing problem is documented starting in 1989; and, being a member of the top five cotton pest problems, aphids represent a significant insecticide resistance problem.

Unseen in these figures is the gradual increase in whitefly problems that occurred in parallel with the aphid population increases. Both of these species are believed to have increased in numbers recently because of insecticide-induced killing of beneficial insects (Newsom and Smith, 1949; Kerns and Gaylor, 1991). Whiteflies and aphids have thus acquired resistance to certain insecticides before becoming significant pests which must now be taken into account in designing treatment strategies (Byrne *et al.*, 1992).

In the San Joaquin Valley of California, the predominant pests, and potential resistance problems, are spider mites (*Tetranychus* sp.), and occasionally the western lygus bug, *Lygus hesperus* Knight. The beet armyworm and cabbage looper can be found occasionally in cotton, but never consistently. Only rarely do tobacco budworm or bollworm present problems, even though both are present on other hosts in the area (Anonymous, 1984; Tom Leigh, 1993, personal communication, University California [Davis], Shafter, CA).

The western lygus bug has gradually developed resistance to insecticides over the years. By 1953, resistance was reported to DDT (Andres *et al.*, 1955). During the 1960s resistance to other organochlorines and to several widely used organophosphates was established by Leigh and Jackson (1968). The list of resistant compounds was extended by Leigh *et al.* in 1977. Presently, acephate (Orthene®), methamidophos (Monitor®) and dicrotophos (Bidrin®) are effective as foliar sprays against the western lygus bug while methidathion (Supracide®) is not always highly effective, suggesting the development of resistance.

In desert growing areas of California and Arizona, the pink bollworm, *Pectinophora gossypiella* (Saunders), is the key pest of cotton (Anonymous, 1984). Since about 1966 the pink bollworm has been distributed from Texas across New Mexico and Arizona to southern California and in adjacent Mexican cotton fields. Although the pink bollworm distribution covers almost the entire western part of the Cotton Belt, its seriousness as a pest problem, and therefore as a resistance threat, varies drastically (Noble, 1969).

In West Texas and from El Paso east along the Rio Grande Rider, the pink bollworm has been held in check largely by cultural control practices including adoption of a short growing season strategy (Bottrell and Adkisson, 1977). Further up the Rio Grande at Las Cruces, New Mexico, the pink bollworm is a late-season pest, probably because it does not overwinter locally, but rather reinvades each year from warmer climates downriver. The same is true at the higher elevations of central and eastern Arizona, where only a few spray treatments may be necessary to control pink bollworm yearly.

Attempts to control the pink bollworm have caused some resistance problems in the past, but given the amount of insecticides used to control pink bollworm yearly in the chronically infested areas, and given the large endemic populations, it is remarkable that resistance problems have not been more severe (Haynes, *et al.*, 1986, 1987; Bariola, 1985; Bariola and Lingren, 1984).

Attempts at chemical control of the pink bollworm have often led to secondary outbreaks of tobacco budworm, cotton leafperforator, *Bucculatrix thurberiella* Busck, and sweetpotato whitefly. The insecticide-induced secondary pest problems in the Imperial Valley of California have become especially severe since 1981 with the insecticide resistant whitefly (Prabhaker *et al.*, 1988; Youngman *et al.*, 1986) building up in cotton in the fall and fouling the lint with honeydew which allows growth of sooty mold. The whitefly later transmits lettuce yellows virus to lettuce and melon crops into the late fall growing season.

While the bollworm is relatively abundant in the cotton growing areas of Arizona and California, it is not an important or chronic pest of cotton. The tobacco budworm is difficult to find in the southwestern desert cotton growing areas of the United States until usually in mid-August when numbers increase markedly, but it, too, is an inconsistent pest of cotton in the southwestern desert.

The tobacco budworm and bollworm are key pests in the Mid-South and eastern cotton growing areas of the United States. This includes the area in Texas along and north of the lower Rio Grande River; the delta growing area roughly bordering the

Mississippi River at and near the juncture of the states of Louisiana, Arkansas and Mississippi; and to a lesser extent the additional cotton growing areas of the Cotton Belt from Mississippi further east through Alabama and Georgia to South and North Carolina.

The boll weevil has been a traditional cotton pest also in the Southeast and Mid-South sections of the Cotton Belt. For the past several years the USDA has been conducting a boll weevil eradication program that reports to be successful starting in North Carolina (Cousins, 1991). In the West, the boll weevil became a problem in the first half of the 1980s when infestations were noted in many cotton growing areas bordering the Colorado River. Eradication attempts started in 1985 and were successfully completed along the Colorado River including Mexico a few years later (Cousins, 1991).

Therefore, boll weevil is no longer a significant pest in cotton growing areas of the far western United States. The boll weevil is also reduced as a pest in the greater Rio Grande Valley of Texas where cultural control in the form of short-season strategy keeps the pest in check (Bottrell and Adkisson, 1977).

In South Carolina, the only recommended treatment for infestations of both the boll weevil and budworm in the same field was the (2:1) mixture of methyl parathion and EPN. This is due to the relative ineffectiveness of pyrethroid insecticides against boll weevil. Although installing a resistance management program aimed at boll weevil has crossed many minds in the past, one has never been developed. The boll weevil eradication program as conducted by the USDA is simplicity itself, extensive monitoring locates the weevil, then localized blanket spraying with malathion follows and this program is repeated at a low population trigger for spraying.

Malathion control of the boll weevil has not shown any tendency to decline in effectiveness. It is reported that, unlike the larval stages, the adult boll weevil lacks any mechanism with which it can develop resistance to organophosphorus insecticides (Brattsten, 1987a,b). Although there are few reports of boll weevil resistance, Teague *et al.* (1983) did report a 3- to 6- fold tolerance to azinphosmethyl (Guthion®) in a field strain obtained from the Lower Rio Grande Valley. The work was done in response to grower reports of problems controlling boll weevil.

In the Southeast, the ecology of cotton pests is quite different from the West, with smaller fields of non-irrigated cotton often surrounded by wooded areas or other crops such as soybean, corn or tobacco. Damage from bollworms and budworms is just as severe in the southeastern states of North and South Carolina and Florida as it is in Texas, Louisiana, Arkansas and Mississippi.

The tobacco budworm is generally more difficult to control in cotton than the bollworm. It is often the predominant species once insecticides have been applied, and it must be considered the more serious threat to the crop, i.e., the more endemic. The tobacco budworm was more resistant against 10 of 13 insecticides when tested on both species (Sparks, 1981). The three compounds against which tobacco budworm was more susceptible were permethrin (Ambush®, Pounce®), fenvalerate (Pydrin®) and carbaryl (Sevin®). However, these data were gathered soon after the introduction of pyrethroid insecticides, and the situation changed within a few years when tobacco budworm resistance to pyrethroid insecticides developed (Plapp *et al.*, 1990).

It is highly instructive that pyrethroid resistance did not develop in the bollworm when budworm resistance was documented. Although both of these major cotton pests are present in cotton, they are also pests of a range of other crops, e.g., bollworm on corn and tobacco budworm on tobacco. There is some speculation that host selection plays a role in this process, as the bollworm would tend to maintain a reservoir population of individuals susceptible to insecticides on untreated corn, its preferred host. The same speculation assumes that the tobacco budworm would remain on cotton and therefore under greater selection pressure.

A vital clue to the response by the tobacco budworm to insecticides comes from population studies. With a dividing line somewhere around New Mexico or West Texas, tobacco budworm populations in the United States are said to split into western and eastern prototypes (Sluss and Graham, 1979). This study was based on about 16 locations and may not have resolved other subpopulations which might be revealed by considering many more locations. This possibility might explain why the tobacco budworms are key pests east of this line and not in the Far West.

Identification of species is at the heart of both resistance management and insect pest management. Insecticide resistance spreads most rapidly in a fully interbreeding population. Substrains of populations might have the effect of delaying resistance by holding a critical mass of susceptible genes away from selective pressure in ordinary cropping cycles. It is possible that the bollworm is doing a similar thing by its host selection behavior.

Defining a possible subpopulation of a pest insect was shown to be vital in the study of another major new cotton pest, the older sweetpotato whitefly. After considerable study, this very old cotton pest was determined to be present in two forms, termed strains A and B. The name silverleaf whitefly was recently suggested for the B strain to show its uniqueness and virtual isolation from the original species (Perring *et al.*, 1993).

It is suspected that these two strains are reproductively isolated one from the other. There is continuing debate and disagreement over whether sweetpotato and silverleaf whiteflies are actually different species or not, but the debate merely underlines the critical importance of understanding the biology of pest populations, and the fact that insect populations are dynamic, ever changing, and unpredictable from year to year.

RESISTANCE MANAGEMENT TACTICS AND STRATEGIES

The genetic bases of most types of resistance have been determined. We know within a few genetic map units where the various factors for resistance map to specific loci on chromosomes (Plapp, 1976; Oppenorth, 1985). Although most of this information comes from house fly, *Musca domestica* L., whose major advantage is a short enough generation time to make inheritance studies practical, it is tacitly assumed that major resistance mechanisms in other insects have similar bases.

Recently, it was documented that repeated copies of a single gene (a process termed gene amplification) exist in resistant green peach aphids, *Myzus persicae* (Sulzer). While the details of how these repeated copies of the same gene might come about and

how they are activated is currently being studied, it is clear that the insect can synthesize large amounts of single resistance factors such as the esterase enzyme in this case (Devonshire and Field, 1991). The pertinent fact concerning this particular esterase resistance is that it confers cross resistance to pyrethroids, carbamates and organophosphorus insecticides.

While genetic knowledge of this kind has been useful in designing resistance management strategies (Denholm and Rowland, 1992), all tactics used in resistance management schemes are, of necessity, based on those parameters that are within the control of practitioners. Characteristics of the biology of pest insects, for example, that are not manipulatable by cultural or other control approaches must, of necessity, be ignored. What remains is often termed operational factors and these include selection of insecticides, timing and dosage of treatments, area treated and application method (Denholm and Rowland, 1992; Plapp, 1993).

One drawback of these tactics in resistance management is their implied emphasis on chemical control. The best way to manage resistance to insecticides, of course, is to reduce their use drastically and develop truly integrated pest management approaches. It is difficult at the best of times to develop an integrated insect pest management approach because IPM is considerably more difficult to achieve than chemical control. The cotton industry as a whole seems reluctant to adopt newer technologies.

THE AUSTRALIAN PYRETHROID STRATEGY

The most pertinent resistance management program to cotton production in the United States, aside from its own, was the one initiated by the Australian cotton growers in 1983 and was designed to prevent the spread of tolerance to pyrethroid insecticides by *Helicoverpa armigera*.

The Australian strategy (outlined in modified form below) was relatively simple. It was designed to restrict the use of pyrethroid insecticides to one generation of *Helicoverpa armigera* per season. Although the strategy was simple, adopting it was not. All growers of summer crops in a large area of Queensland and New South Wales had to be convinced to adopt the strategy. Because *Helicoverpa armigera* is a multihost pest, selective pressure had to be removed from all sources to be successful. In particular, sorghum growers enjoyed excellent success with a single treatment of a low dose of pyrethroid to control sorghum midge, and the pyrethroid strategy meant they would lose this tool in the middle of their season.

Australian Resistance Management Strategy (1983):

Stage I	Stage II	Stage III
(first spray to Jan. 9)	(Jan. 10 to Feb. 20)	(Feb. 21 to last spray)
endosulfan	endosulfan	no endosulfan
monocrotphos	BT/chlordimeform	methomyl
profenofos	profenofos	profenofos

no pyrethroids	methomyl	no pyrethroids
methomyl	pyrethroids	parathion
sulprofos	sulprofos	thiodicarb

In addition to the voluntary restriction in time of both pyrethroids and endosulfan, growers were urged to use no more than three pyrethroid sprays in mid-season during the allowed period. They were also urged to use at least three different groups of insecticides distinguished as having unique modes of action as shown below:

Group A: Endosulfan (Thiodan®) (a cyclodiene acting at the GABA synapse).

Group B Organophosphorus compounds (cholinesterase inhibitors) including sulprofos (Bolstar®), profenofos (Curacron®), acephate (Orthene®), parathion, and monocrotophos (Azodrin®).

Group C: Carbamate insecticides (cholinesterase inhibitors) including thiodicarb (Larvin®) and methomyl (Lannate®, Nudrin®).

Group D: Pyrethroids (acting on the sodium channel) including fenvalerate (Pydrin®), cypermethrin (Ammo®, Cymbush®) and deltamethrin (Decis®).

Group E: (miscellaneous) delta endotoxin of *Bacillus thuringiensis* (Berliner) and chlordimeform (Fundal®, Galecron®).

All results reported to date suggest that the Australian resistance management strategy designed to delay the development of resistance to pyrethroid insecticides has worked (Croft, 1990), despite some early skepticism (Davies, 1984). A five-year continuous survey of discriminating doses showed that resistance to pyrethroids built in mid-season when pyrethroid use was allowed, but the resistance then declined by the start of the subsequent growing season, although usually somewhat above the original level (Roush and Daly, 1990). This phenomenon has been referred to above as a "rachet up" effect and can be seen also in the first few years of monitoring data of cypermethrin resistance in tobacco budworm in the Mid-South and Texas (Mullins *et al.*, 1991) where it is termed a "stair step" annual increase (Rogers *et al.*, 1991).

The pattern of resistance build up and decline was first seen in the Australian situation because of a vigorous resistance monitoring program that was supported by the Australian cotton growers. Resistance monitoring has since become more widespread in cotton growing areas of the Mid-South of the United States and the same results seem to hold true (Clower *et al.*, 1992). Indeed, resistance is now suspected of occurring frequently during the cotton growing season (Rogers *et al.*, 1991).

THE ZIMBABWE RESISTANCE MANAGEMENT STRATEGY

The first nationwide resistance management program for cotton pests was developed in Zimbabwe while it was still Rhodesia in 1972-1973 (Duncombe, 1973). The Zimbabwe plan was devised due to dimethoate resistance that developed in carmine spider mites, *Tetranychus cinnabarinus* (Boisduval) and *Tetranychus lombardinii* Baker and Pritchard.

Critical to these events was a reliable resistance testing scheme which had been developed by 1968. When testing revealed mite resistance to monocrotophos (Azodrin®), one of the few remaining acaricidal compounds available, a rotation scheme was devised:

The Zimbabwe Scheme (Sawicki and Denholm, 1987):

(1) Formamidine and carbamate used for two seasons.
(2) Chlorfensulfide and chlorfenthol (Quibrom®, Dimite®) used for the next two seasons,
(3) Monocrotophos (Azodrin®) and triazophos (Hostathion®) used for the next two seasons; and
(4) Return to (1) above, and continue...

In addition to the rotation scheme shown above, endosulfan (Thiodan®) was recommended for bollworm control instead of DDT which was known to induce mite population flare-ups. Formamidines and carbamates were put into the strategy because they were shown to have increased efficacy on organophosphorus resistant mites in a valuable and fortuitous discovery of negatively correlated resistance development (Dittrich, 1969).

The Zimbabwe scheme was voluntary and achieved success over an extended period of time. Considerable care was taken to explain the program and enlist the support of the growers and agrochemical industry. Competition between agrochemical companies resulted in the country being divided into six, then later three regions so that all of the groups of recommended products were actually used in any given year. The regions were separated enough to ensure an interruption in the flow of resistant gene pools.

When chlordimeform (Fundal®, Galecron®), the formamidine used in the beginning of the strategy, came under regulatory scrutiny for adverse health effects, it was replaced by another formamidine, amitraz (Ovasyn®), with a similar mode of action and chemistry.

After the experience with spider mite resistance, Zimbabwe officials anticipated potential problems expected from the introduction of synthetic pyrethroids in 1977-1979. They directed that cotton growers use pyrethroids only during a defined period of not more than nine weeks that coincided with the maximum flowering period when most pest pressure from bollworms occurred (Blair, 1986). Three winter months were designated as pyrethroid free.

When the Australians decided to develop a pyrethroid resistance management strategy in 1983, they borrowed from the Zimbabwe experience. Indeed, one of the principle architects of the Zimbabwe scheme, John Brettell of the Cotton Research Institute at Kadoma, was invited to Australia to assist in the inauguration of the Australian strategy. Although he could not accept because the African growing season coincides with that in Australia, it turned out that the growers in Australia as a whole were far more amenable to the plan than the industry leaders realized and readily adopted it, as confirmed by its continued success (Croft, 1990).

PYRETHROID RESISTANCE IN TOBACCO BUDWORM IN THE UNITED STATES

Resistance to pyrethroids occurred in the United States in the tobacco budworm similar to the event in Australia and only a few years later. Like Australia, many United States growers had been using exclusively pyrethroids for pest control since their introduction to cotton pest control in the mid-1970s. For the first ten years of pyrethroid insecticide use in the United States, there was no attempt by growers to develop resistance management approaches despite very clear warnings about the consequences (Elliott *et al.*, 1978; Sparks, 1981).

Indeed, up until and even after the first reports of resistance to pyrethroids from the Winter Garden area of Texas, 100 miles west of the city of San Antonio, many refused to accept the reports and were openly skeptical (Staetz, 1985; Plapp *et al.*, 1990; Plapp, 1991). Nevertheless resistance was soon accepted by all concerned, and a resistance management scheme was initiated soon after.

The Tri-state Resistance Management Scheme—The elements of the Tri-state strategy (named for the regions represented by the framers in Louisiana, Arkansas and Mississippi) are fairly straight forward (Anonymous, 1986; Certain, 1988; see also Rogers *et al.*, 1991). The three elements are:

(1) Plant and protect early, harvest early;
(2) Use no pyrethroids until June 30; and,
(3) After July 1, use pyrethroids as necessary until August 15, although there are some local variations (Anonymous, 1990a).

This approach was designed to remove selective pressure by pyrethroids from the first generation of the tobacco budworm/bollworm complex. However, the plan also recommends using mixtures of insecticides, a recommendation that does not have universal acceptance (see section below on using insecticide mixtures).

The Tri-state strategy was adopted from Texas to Alabama with some regional modifications to the exact pyrethroid-free period. Also, the strategy was complicated by local boll weevil eradication procedures being conducted in Alabama, for example (Certain, 1988). One of the arguments used in favor of some self-regulation of pyrethroids was financial. Loss of the relatively inexpensive but effective pyrethroids through resistance would necessitate use of more expensive materials (Anonymous, 1990a). Thus, cultural practices that encourage earliness were stressed along with early harvest.

The adoption of resistance management strategies requires cooperation on a scale not ordinarily practiced in farming communities. One natural characteristic of farming communities is a friendly competition or rivalry between growers. Therefore, it is in a very real sense unnatural for growers to cooperate in an endeavor that involves the way each individual farms, in this case how each individual controls insects. Early indications suggest a less than uniform compliance to the Tri-state strategy on the part of the growers (Croft, 1990; Rogers *et al.*, 1991).

THE ENVIRONMENTAL MOVEMENT AND CONSEQUENCES

The key element that caused the Australians to cooperate and overcome natural competitive instincts was the specter of losing effective insecticides. The worldwide outcry against pesticides that began in 1964 and grew into what we refer to as the environmental movement has wrought much change. The most pertinent change was to add constantly changing layers of governmental regulation to the registration of pesticides with all costs passed on to agrochemical industry.

This has had the effect of temporarily reducing the number of new insecticides (Finney, 1991; Voss and Neumann, 1992). Because the costs are so much higher, searching for new materials is even more of a gamble than before (Voss and Neumann, 1992). As a result the agrochemical industry has undergone, and continues to undergo, a dramatic contraction. Shell agrichemicals in the United States was acquired by DuPont some years ago. Dow and Eli Lilly merged into DowElanco; Sandoz purchased Zoecon, and more recently Wellcome Environmental Health was purchased by Roussel Uclaf and FMC was acquired by Monsanto, to name a few mergers.

It has been projected that by the turn of the century there may be only five very large chemical firms left in the business of marketing pesticides. While growers may begin to see fewer familiar and traditional pesticides, the market for insect control agents has not changed that much yet. The cotton industry still accounts for the lion's share of pest control sales in the United States.

Agrochemical companies have been quietly investigating potential new products under the umbrella of "biopesticide." Biopesticides are said to include pheromones, attractants, microbials and some lists even include the neurotoxic pyrethroids (Simmonds *et al*., 1992; Anonymous, 1990b; Voss and Neumann, 1992). The non-pyrethroid portion of the biopesticide market was recently projected to grow 11 percent through the year 2000, and to reach US$300 million in sales by 1999. A growth of 15 percent per year was also predicted for sales of bacterial-based pesticides in particular (Anonymous, 1990b), but Marrone and Macintosh (1992) put these at one percent of the world market.

Although this prediction appears rosy at first glance for non-neurotoxic insect control agents or chemicals, reality suggests something else. Perceived as replacements for the present range of neurotoxic carbamates, organophosphorus and pyrethroid insecticides (Hutchins and Gehring, 1993), the biologically based materials that act as growth regulators, behavior modifiers, or bacterial or viral toxins are considered (Voss and Neumann, 1992; Wood and Granados, 1991) "...unreliable, uneconomic, and of a very limited practical value."

The projected world sales of insecticide products is reportedly US$ 7 billion by 1995 (Voss and Neumann, 1992). The non-neurotoxic insecticide part of this is projected to be less than 10 percent. Representatives of agrochemical industry have been quietly pointing out these realities for some years, but the message does not seem to be getting through (Hutchins and Gehring, 1993).

THE MEASUREMENT OF INSECTICIDE TOXICITY

PROBIT ANALYSIS

When most parameters or physical traits are measured in a homogeneous population, the results, when plotted, form a bell-shaped curve, or Gaussian distribution. The measurement of toxicity of a given insecticide is no exception. Since toxicity of a given chemical is measured in populations rather than individuals, a special type of statistical procedure termed probit analysis is used.

Resistance determinations are basically comparisons. Some of our colleagues concern themselves with defining resistance (cited from Muggleton, 1984), which is fundamentally important. To have solid and useful information from field pest insects, one must have reference values to begin with, or a stable susceptible reference population. Although seemingly straight forward, a susceptible population can be rare, difficult to obtain or non-existent. This is especially true of pest insects that are not readily cultured, or new strains that become *de novo* (anew) pest insects.

It is generally appreciated (cited from Gould, 1984, 1991; Devonshire and Field, 1991; Ronis and Hodgson, 1989) that insects have been evolving defense mechanisms against plant toxins as long as both have been co-evolving. Most of these involve metabolic factors, but a host also undoubtedly involves feeding behaviors as well. So one may well wonder what susceptibility really is in the first place.

Probit analysis plots the mortality caused by insecticides in a population of insects against the logarithm of doses used. The probit technique changes the bell-shaped nature of the results into straight lines that are more convenient for analysis. Probit programs are now available that run on personal computers (Raymond, 1985).

The probit analysis of a given insecticide against a homogeneous population will yield a straight line. In the example shown here (Figure 1), the toxicity of fenvalerate (Pydrin®) to a susceptible population (S) is plotted alongside the toxicity to a field population of larval *Helicoverpa armigera* (Gunning *et al.*, 1984). If a portion of the population contains one or more resistance traits, the probit or ldp (log dose probit) line shifts to the right (as shown by the arrow in Figure 1). The non-homogeneity of the strain is indicated by the probit line no longer being straight.

If the field strain in Figure 1 is selected by treating several generations with a dose causing 70 percent mortality (the LD_{70}), then the population would become homogeneous for resistance, and the probit line would be straight, but shifted to the right (indicated by the dashed line labelled R in Figure 1). The log dose probit (ldp) lines of the S and R strains shown in Figure 1 are separated horizontally by about 100 dosage units at their mid points, so we consider the R strain to be 100-fold resistant compared to the susceptible S strain. Therefore, while resistance is developing, the probit lines reflect the change and the heterogeneity of the population by bending to the right at the top.

Note also that the LD_{50} (50 percent mortality) value of the field strain does not show the potential resistance fully. In the example shown, the LD_{50} values of the susceptible strain and field strain are less than 10 dose units apart.

Log probit data are most accurate near the 50 percent mortality points and increasingly less accurate at both lower and higher mortality points. This is the main reason why the LD_{50} value has become the standard measurement for toxicity. But this value only has meaning for homogeneous populations. In most cases, field populations are not homogeneous.

If one percent of a field population contains highly resistant individuals, a probit analysis will yield a line that is very similar to the susceptible line shown in Figure 1, with perhaps a few values far off the curve at the upper end depending on how many insects were tested. The important information about the few individuals that are resistant will almost certainly be lost, even if a very large number of insects is tested for toxicity. This is a limitation of the probit method, and reflects the difficulty of determining resistance.

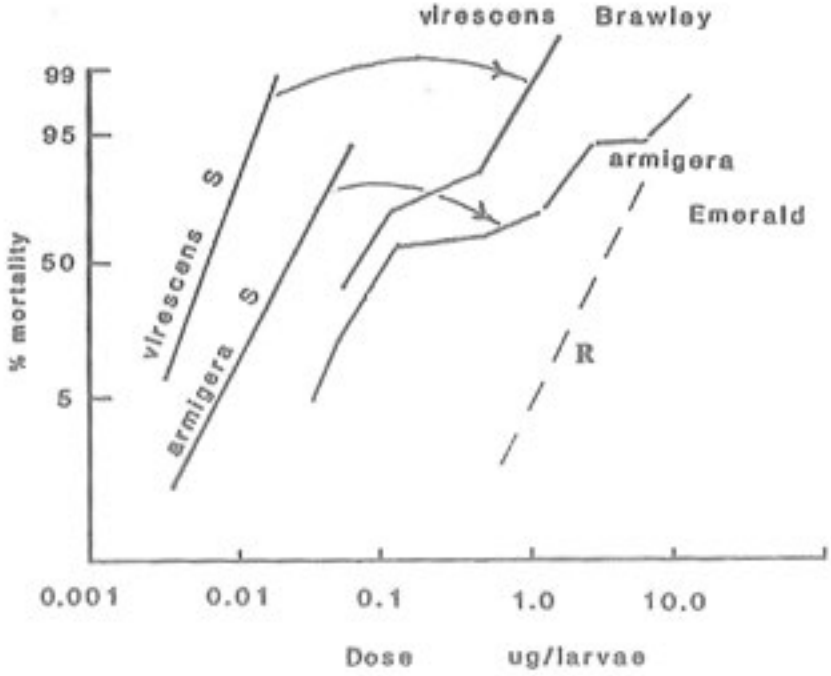

Figure 1. Toxicity of fenvalerate (Pydrin®) to third instar tobacco budworm from Brawley, California and bollworm from Emerald, Queensland, Australia. The log probit plots of susceptible (S) and field collected (lower arrow) *Heliothis armigera* were taken from Gunning et al. (1984). The dashed line (R) shows the result expected if this field population were pressured for several generations by fenvalerate until homogeneous for resistance. Also shown are probit data from susceptible (S) *Heliothis virescens* (tobacco budworm) and from a field strain (upper arrow) collected near Brawley, California in 1984. (Tom Miller, unpublished data.)

To help overcome some of the limitations in log dose probit analysis, a discriminating dose can be used as a diagnostic tool. If the population labelled S in Figure 1 were treated with twice the dose needed to produce 95 percent mortality (two times the LD_{95}), there should be no survivors. If this same discriminating dose were used to treat the field strain, nearly half the population would survive the dose. It can be seen that this is a practical way of rapidly estimating resistance in the field.

To generate the probit line, one needs at least four doses plus a control and at least one replicate. At 20 insects per dose, this amounts to a minimum of 200 insects. One can appreciate that the discriminating dose technique is considerably simpler to perform. However, large samples are still required to document the low percentages of resistant individuals in some populations (Roush and Miller, 1986). Of course, to obtain more detailed information, the probit method must be used, but it is no surprise that the Australians, and later, the Americans, adopted the discriminating dose method in their resistance monitoring programs.

QUASI-SYNERGISM AND PHYSICAL ARTIFACTS

Aside from the drawbacks of probit analysis, there are other complications that are important to keep in mind when trying to determine toxicity. In a classic paper that often escapes notice, Sun and Johnson (1972) documented an artifact in the determination of toxicity of carbaryl (Sevin®) to house flies. When topically applied in acetone, carbaryl gave a toxicity of 900 micrograms per fly. However, when formulated in kerosene and reapplied in exactly the same way, the toxicity was 1.1 micrograms per fly. Sun and Johnson termed this phenomenon "quasi-synergism" because it appeared as though carbaryl toxicity had somehow "improved."

In fact, some insecticides, when applied in acetone, have a physical habit of crystallizing on the cuticle, and thus being unavailable for penetration. This reduces the toxicity of topically applied compounds by an amount that is directly attributable to how much material precipitated on the surface. In some cases this is not significant (Schouest *et al.*, 1983), but in others it is important. Since no insecticides are formulated in acetone, this problem rarely occurs in field applications; instead, it is almost always a possible artifact in the laboratory, where the use of acetone is common.

Probably Sun and Johnson (1972) were experiencing carbaryl precipitation on the surface of the house flies. Whatever the cause, from the time quasi-synergism was discovered, Shell Development Company, where the work was done, switched from routine use of acetone in testing to the use of kerosene. Insecticides such as organophosphorus insecticides, or any other materials that are oily at room temperature, would naturally not have these peculiar physical properties. However, the concept of quasi-synergism is always important to remember when assessing insecticide toxicity.

TYPE OF RESISTANCE

Four major factors responsible for resistance are listed below. They are considered to be the main means by which pest insects develop tolerance to insecticides, and they

can be measured with ease or difficulty. To understand the nature of resistance monitoring, and the strategies behind resistance management, one must be familiar with these factors:

(1) Behavior;
(2) Penetration;
(3) Altered site of action (kdr, AChE); and,
(4) Metabolism (oxidase, esterase, hydrolase, transferase...).

Each of these types of resistance has been demonstrated or measured. For practical purposes, most of these factors of resistance can be considered traits that are genetically inherited. It is popular to consider the development of resistance as an example of Darwinian evolution in action, i.e., survival of the fittest in the face of selection by insecticides.

BEHAVIORAL RESISTANCE

Behavioral resistance means the pests have inherited a behavior pattern that somehow causes them to avoid a toxic dose (possibly by staying on a part of the plant that is protected from exposure to chemical sprays, for example). This type of resistance is the most difficult to measure. Many reports of behavioral resistance are anecdotal observations. Groups of pest insects are seen to be residing on different parts of the plant, such as whiteflies occupying the lower third of the mature cotton plant in late season (Personal communication, N.C. Toscano, University of California-Riverside) or horn fly residing on an untreated part of the steer (Lockwood *et al.*, 1985).

When taken in to the laboratory, it can be appreciated that these insects would test as susceptible by accepted toxicological testing procedures using topical applications of precise amounts. All too often the bioassays are designed for the convenience of the experimenter and miss the more subtle or esoteric forms of resistance. Another view of these groups of insects is that they can represent a pool of susceptibility for diluting the other forms of resistance, assuming they are not already cross-resistant themselves.

Some insects evolve behavioral avoidance of antibiotic crop cultivars which may be an important principle in developing insect resistant varieties (Gould, 1984). Lockwood *et al.* (1984) described behavioral resistance as either stimulus-dependent or stimulus-independent, but they also defined protective avoidance as distinct from behavioral resistance. They gave a number of examples.

Gould (1991) considered that either insecticides with repellent properties or insecticides used with insect repellents can significantly decrease the rate of development of resistance. The entire field of the behavioral response of insect to selective pressure is a much neglected field of study (Lockwood *et al.*, 1984).

PENETRATION RESISTANCE

Penetration usually is not a big factor in resistance and is more readily measured. In some cases insecticides simply do not penetrate inside the resistant insects as rapidly as in a comparison (susceptible) strain. The most convenient way to determine this

information is to measure the rate of uptake of radiolabelled insecticide from topical treatment (Sawicki and Lord, 1970). This can be done by topically applying the labelled insecticide to both susceptible and suspected resistance individuals, then washing the cuticle with solvent after a short wait and comparing amounts of unchanged insecticide (Nicholson and Miller, 1985).

To split hairs, this procedure actually measures what is left on the surface of the insect, not how much actually penetrated and became available as primary toxicant inside. However, determining the latter requires a more extensive toxicological research project. Given the dwindling support for insect toxicology, the effort required may not be justified.

ALTERED SITE OF ACTION RESISTANCE

An altered site of action means the site where the insecticide exerts its primary toxic action is somehow genetically altered so that greater amounts of the insecticide are now needed to produce the same effect as previously.

The term "kdr" means "knock down resistance" to pyrethroid insecticides. Insects with kdr-resistance either do not respond at all to a dose that normally kills the susceptible strain, or the symptoms of poisoning take far longer to appear than in the susceptible strain. In this case the first symptoms of poisoning are termed knockdown. In the case of DDT and pyrethroids, the presence of a kdr-like resistance mechanism normally requires sophisticated electrophysiological equipment for final confirmation. However, kdr-like resistance can be measured by simpler methods as long as complicating factors such as penetration do not interfere with the interpretation.

The kdr-resistance mechanism was originally demonstrated by Busvine (1951) for DDT. Table 3 shows the very simple results reported by Busvine from three house fly, *Musca domestica* L., strains, one susceptible, one with kdr-like genes and a third strain with largely metabolic based resistant genes against DDT. Note that the kdr-like factor was expressed very fast, within minutes of treatment, by a lack of response compared to the susceptible or metabolic resistant strains when all strains were treated by the same dose.

Table 3. Percent of adult female house flies knocked down after exposure to DDT residues (0.1 mg/cm^2) in a 500 ml beaker. (After Busvine, 1951.)

Knockdown time	Strains		
	Rome susceptible	Italian resistant	Sardinian resistant
	(%)	(%)	(%)
Down in 20 minutes	35	0	27
Down in 40 minutes	93	11	80
Down after 24 hours	100	8	11

The hallmark of metabolic resistance is eventual recovery many hours following poisoning. As seen from the information in Table 3, it can be appreciated that the initial responses to poisoning of the susceptible strain and the strain containing metabolic resistance are similar, and major differences express themselves only many hours later.

It was shown that the kdr-like factor is expressed throughout the nervous system. Motor nerve terminals of larval house flies with the kdr-like gene expressed a resistance to pyrethroids (Salgado *et al.*, 1983a,b). The central nervous system also expressed a resistance to pyrethroids in the same strain of house flies with the kdr-like gene (Miller *et al.*, 1979).

Although the symptoms of insecticide poisoning normally express themselves within the first 30 minutes of topical treatment, the ultimate toxicity depends on what happens many hours later. This principle of toxicology is best illustrated by considering unpublished results from Dr. Harry von Keyserlingk of Schering AG in Berlin (Figure 2).

Deltamethrin (Decis®), considered the most toxic of all the pyrethroid insecticides, knocked down adult house flies minutes after topical application (Figure 2). Over a period of seven days, however, the number of insects remaining down began to decrease until about 80 percent fully recovered. If, on the other hand, the deltamethrin dose was delivered along with a nontoxic amount of the synergist, piperonyl butoxide, which blocks oxidative metabolism, the adults never recovered during the following week.

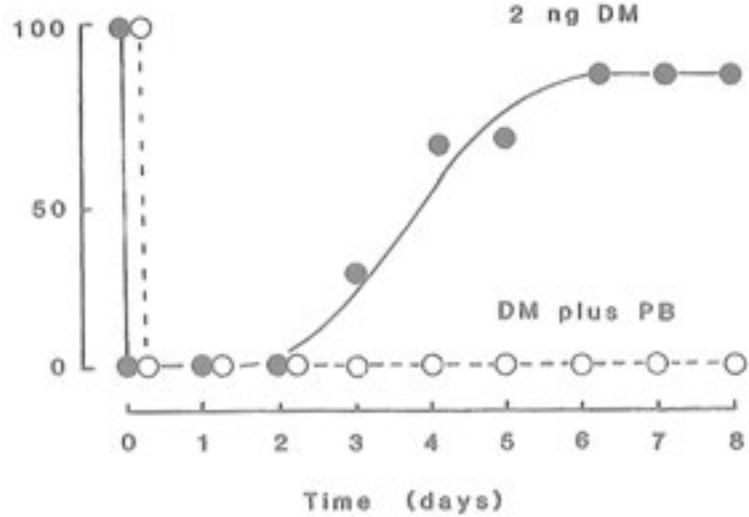

Figure 2. Recovery of adult house flies topically treated with 2 ng DM [deltamethrin (Decis®)] (From Dr. Harry von Keyserlingk, Schering, AG, Berlin). Note recovery took longer than two days to begin even though toxicity is normally determined after 24 hours. In presence of the synergist, piperonyl butoxide (PB), the adults never recovered from the same dose of deltamethrin.

This simple experimental result from Schering shows a powerful concept in a simple example. First, pyrethroids do not "kill" insects. Put another way, insects can survive massive chemical insult to their nervous systems. Secondly, given time, the metabolic machinery of insects can reduce the concentration of active ingredients in the hemolymph (blood-like circulatory fluid in insects) to below toxic levels allowing the insect to recover. Many investigators measure toxicity 24–72 hours after treatment, and ignore longer term recovery.

The important lesson to learn from Figure 2 is that the main metabolic component in insecticide poisoning takes a long time, many hours or even days to fully express itself. It never happens immediately. As shown by Busvine (1951), however, the presence of a kdr-like resistance factor can be tested for in minutes. This fact was the principle upon which the "warm-needle" bioassay for kdr-like resistance was developed. The warm-needle assay was perfected by Jeff Bloomquist (Bloomquist and Miller, 1985, 1986). Figure 3 shows results of this procedure applied to larval house flies.

Following topical treatment, a group of maggots were "probed" at regular intervals. Those failing to respond were scored as paralyzed and the percent paralyzed was recorded over time. Within an hour following topical treatment, larvae with kdr-like genes were easily distinguished from susceptible insects. The amount of kdr-like gene expression was also readily apparent (Figure 3). In the example shown, the resistant

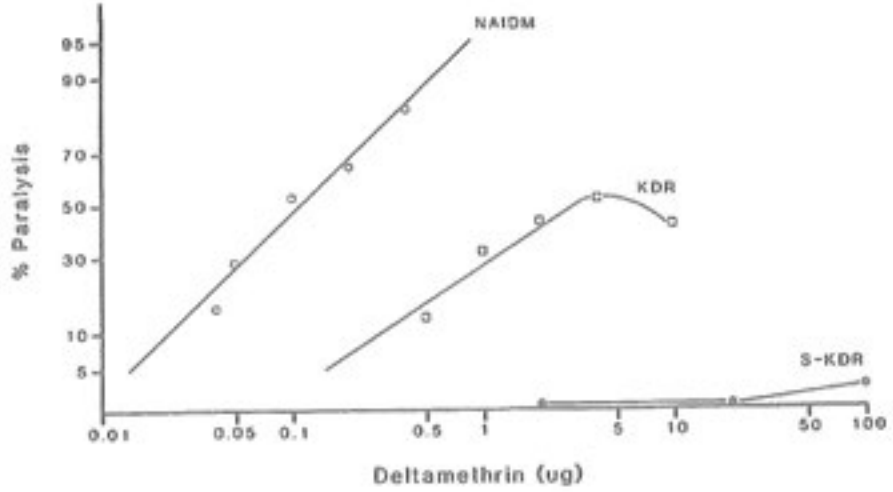

Figure 3. Dose response of deltamethrin (Decis®) topically treated on third instar house fly larvae from three different strains (From Bloomquist and Miller, 1986). Paralysis was determined ten minutes after treatment. The strains are susceptible (NIADM), and 100-fold resistant (S-KDR) and 10-fold resistant (KDR) both of which were selected for single gene kdr-resistance.

strains were 10-fold and 100-fold resistant to deltamethrin (Decis®), respectively, compared to the susceptible strain based on the ratios of the LD_{50} values.

The warm-needle assay was adopted for studies on pink bollworm, and perfected for the horn fly (Crosby *et al.*, 1991). The same principle can be used to demonstrate a kdr-like gene or effect in any insect. Thus, as originally demonstrated by Busvine (1951), the presence of a kdr-like factor can be determined in minutes in any convenient assay. This is essentially what is being done in the vial assay as it was adapted to resistance monitoring of the whitefly (Staetz *et al.*, 1992). In this vial assay, adults are held only a few hours before toxicity is determined. As can be seen from the arguments above, kdr-like resistance would be readily apparent in this assay, but metabolic resistance would not.

Altered site of action resistance to organophosphorus or carbamate insecticides involves an alteration in cholinesterase (ChE), the target enzyme. This normally requires laboratory analysis by biochemical means for final confirmation. In the tobacco budworm, a single gene was shown to be responsible for methyl paraoxon resistant acetylcholinesterase (Brown and Bryson, 1992).

Since the altered cholinesterase factor would be expressed as a general lack of response to cholinesterase inhibitors, it would respond in rapid assay in the first several minutes of treatment in a manner similar to pyrethroid resistant insects with kdr-like mechanisms. While this should be straight-forward to demonstrate with carbamate insecticides, there are technical reasons why it may be more complicated with organophosphorus insecticides (Miller, 1976).

METABOLIC RESISTANCE FACTORS

The final mechanism of resistance, metabolic, is by far the most common and the most complex. Insecticides are basically chemical molecules made up of so-called functional groups. Since most insecticides have a carbon skeleton, nature has a myriad of ways to alter, digest and break apart such structures, usually by enzymatic means. The only exception is the carbon-chlorine or carbon-halide bond which is rare in nature and consequently difficult to reduce. This is the main reason DDT was found to be unacceptable for widespread use; it resisted degradation and eventually accumulated in non- target organisms to unacceptable levels.

It has become popular to point out that insects have been co-evolving for many years with plants. Plants have evolved a spectrum of natural toxins as insect deterrents to which some insects have promptly developed resistance or immunity. The classic case is the tobacco plant with nicotine (an insecticide) and the tobacco budworm. This means that even before insecticides are introduced into crop protection, there are metabolic mechanisms in place that are designed to protect against poisoning.

It is also popular to point out that polyphagous insects (insects that feed on many kinds of food) are more capable of resisting plant toxins presumably because their metabolic machinery is more adaptable. The struggle of coevolution is seen to occur in the larval stages which are largely confined to the locality of their oviposition (egg laying) site. The adult stages not only do not have the same adaptability of metabolic

factors, their diet is considerably simpler. Thus larval stages that are treated, in general, have the greater ability to respond by developing resistance to insecticides (Ronis and Hodgson, 1989; Gould, 1991).

Three main metabolic factors conferring resistance are: (a) mixed function oxidases, (b) glutathione S-transferases, and (c) hydrolases (including esterases) (Devonshire and Field, 1991). All three mechanisms have been demonstrated or are suspected to be present in cotton pest insects (Little *et al.*, 1989; Nicholson and Miller, 1985; Byrne *et al.*, 1992).

Besides insects evolving metabolic and other mechanisms to deal with the natural toxins in plants, the toxins in plants themselves are of great interest. Almost all insecticide products have some remote connection to a natural plant toxin. This even includes the organophosphorus insecticides (Neumann and Peter, 1987). Thus the plants have had to deal with insecticide resistance before through evolution, and perhaps some of their adaptive countertactics might be of some interest in the present context.

SYMBIONT METABOLISM OF INSECTICIDES

A complicating factor in the metabolism of insecticides is the possible activity of symbiotic organisms. Shen and Dowd (1991) reported the presence of esterase enzyme activity in cultures of the yeast-like organism, *Symbiotaphrina kochii* Jurzitza ex. W. Gams and v. Arx., which enjoys a symbiotic relationship with the cigarette beetle, *Lasioderma serricorne* (Fabricius). It was suggested that such symbiotic organisms are able to detoxify a wide range of pesticides, mycotoxins and plant toxins (Shen and Dowd, 1991).

INDUCTION OF METABOLIC ENZYME ACTIVITY

Enzyme induction is a well established phenomenon (Hodgson and Levi, 1987) in which exposure to xenobiotics (foreign chemicals) has the effect of increasing production of certain enzymes to assist in the degradation of the chemical. Diets have been shown to have the same effect. Some of the esterase activity in insects has been shown to be inducible (Yu and Hsu, 1985).

When reared on cotton (Delta Pine 61), corn (Golden Jubilee), chrysanthemum (Florida Marble) or artificial diet (see Shorey and Hale, 1965), tobacco budworm larvae showed little difference in the bands of esteratic activity on gel electrophoresis of hemolymph. Reared on the same host plants, however, analysis of the enzyme activity of the hemolymph of the bollworm showed a greater diet-dependence (Salama *et al.*, 1992).

The bollworm had ten bands of carboxyesterase activity and thirteen bands of cholinesterase activity; whereas, the budworm had eight bands and two bands, respectively, of the same types of enzyme activity. It was concluded that the bollworm larvae with a more diet-dependent esterase activity may have evolved more closely with its preferred host plant while the enzyme complement of the budworm is more stable on different hosts (Salama *et al.*, 1992; Brattsen, 1987a,b).

The toxicity of insecticides on bollworm and tobacco budworm larvae is known to be affected by the diet upon which the larvae are reared. Undoubtedly, enzyme induction in

response to plant chemicals present in specific host plants plays a role in this response to insecticides. Comparing the toxicities of insecticides on the same insect species that originate from different host plants should take these principles into consideration. Bioassay of adult insects alone would certainly miss these subtleties in larval stages.

TYPES OF INSECTICIDE

To understand the development of resistance, the chemistry of insecticide molecules and the exact constituents of insecticides as they are formulated are very important. The Australian resistance management strategy not only restricted the use of pyrethroid insecticides, it restricted the use of endosulfan (Thiodan®) in an effort to preserve this material as well.

The major categories of insecticides are given below to show the common site and mode of action.

DDT and pyrethroid category: DDT, fenvalerate (Pydrin®), permethrin (Ambush®, Pounce®), deltamethrin (Decis®), cypermethrin (Ammo®, Cymbush®), cyhalothrin (Karate®), cyfluthrin (Baythroid®), bifenthrin (Capture®), tefluthrin (Force®), and etofenprox (Trebon®). DDT is sometimes listed as a chlorinated hydrocarbon and incorrectly lumped together with the cyclodienes and lindane (Isotox®). DDT acts at the same site as pyrethroid insecticides. When kdr-resistance was encountered, the original diagnostic test for it was cross-resistance had to be present to all of the other members of this class, i.e., all pyrethroids and DDT.

Cyclodiene category: dieldrin, aldrin, chlordane, heptachlor, endosulfan, lindane, and toxaphene. The cyclodienes include a distinct class of chemicals named after the principle route used in their synthesis, the Diels-Alder reaction. These compounds are now suspected of acting on the chloride ion channel of the GABA synapse. The GABA synapse is named for the neurotransmitter, *gamma* amino butyric acid, that is released at its ending. Endosulfan (Thiodan®) is one of the few compounds of this category remaining in registration for crop protection, and therefore, by virtue of its different mode of action from other major categories of insecticides, is one of the most valuable. The other members of this class were added (lindane, toxaphene, and more recently bicyclophosphates) when their mode of action was discovered.

A nerve cell connects to (or synapses with) other nerve cells (nerve-nerve synapses), muscle cells (neuromuscular synapses), or directly to tissue organs. All nerve cells have neurotransmitter or neuromodulator chemicals that they manufacture and release at their synaptic connections. The release normally occurs when nervous impulses are conducted along the nerve cell axon to its nerve endings or synapses. The nerve cells are normally named by their neurotransmitter chemicals. Thus a nerve that makes and releases *gamma* amino butyric acid (GAB) is a GABA neuron.

When GABA is released at a synapse, it diffuses to the cell downstream (the postsynaptic cell) and excites the postsynaptic membrane, usually after being recognized by a "GABA receptor." Once activated, the GABA receptor in turn causes a brief (milliseconds long) increase in permeability to a specific ion, in this case chloride.

Chloride permeability increases tend to stabilize the postsynaptic cell, or inhibit it from any further activity. Thus GABA neutrons in the central nervous system of insects play a major role in inhibiting other kinds of nervous activity.

Cyclodiene insecticides specifically block the chloride permeability at the postsynaptic membrane of GABA synapses. This leads to an interruption in the inhibitory message and the postsynaptic cells can no longer be inactivated. This is thought to lead to convulsions as motor programs (discrete patterns of nervous activity driving behavior) turn on indiscriminately.

Insects that develop site-insensitive resistance to cyclodiene insecticides are described diagnostically by their cross-resistance to picrotoxinin, a toxic natural product that was used for years to distinguish GABA synaptic transmission. Indeed, all chemical insecticides in this greater cyclodiene category owe their activity to a structural and functional resemblance to picrotoxinin at the site of toxic action in the nervous system. Picrotoxinin acts by selectively and reversibly blocking the chloride ion channel on the postsynaptic membrane of the GABA synapse.

Avermectin category: avermectin. Avermectin is a natural product synthesized by the soil fungus, *Streptomyces avermitilus*. Its structure is so complex that chemical synthesis is impractical. Instead, the product is developed through fermentation tanks and marketed as both a veterinary medicine and an agricultural insecticide product. The outstanding feature of avermectin is that its action on the nervous system seems to be counteracted by picrotoxin. Thus while the cyclodiene insecticides are thought to act by blocking the chloride ion channel at the GABA synapse, avermectin derived products are thought to be active by virtue of increasing the permeability of the chloride channel.

Because avermectin is a natural product that has the unusual property of killing internal parasites in vertebrate animals without harming the host, it is a valuable veterinary product. Being a natural product with a complex structure has hindered development of analogs to avermectin. As a result, the primary manufacturer, Merck Co., Inc., has enjoyed exclusive access to a unique market.

Carbamate category: Carbamate insecticides are considered to be inhibitors of acetylcholinesterase enzyme at cholinergic synapses in the central nervous system of insects. Carbamates were derived from the natural product, physostigmine. The inhibition by carbamates is largely due to a reversible complex formation with the enzyme. Once the enzyme is carbamylated by the insecticide, the carbamate group is hydrolyzed off of the enzyme readily with a half-life of about 25 minutes. This means that poisoning by carbamates is readily reversible, one of the characteristics of carbamate action (Miller, 1976).

Reversibility of carbamylated cholinesterase enzyme, the target of these insecticides, puts carbamates into a different category from organophosphorus (OP) insecticides. The organophosphates act by inhibiting the same cholinesterase enzyme attacked by carbamates, but the half-life of the phosphorylated enzyme is days rather than minutes. Thus the organophosphates insecticides are considered to act longer as insecticides and poisoning symptoms are irreversible, for all practical purposes.

Aryl carbamates category: carbaryl (Sevin®), propoxur (Baygon®), carbosulfan (Advantage®).

Oxime carbamates category: aldicarb (Temik®), methomyl (Lannate®, Nudrin®), oxamyl (Vydate®), thiodicarb (Larvin®).

Members of the oxime carbamate family of insecticides, especially aldicarb, have a unique property in that they are often systemic and are readily taken up and transported in plant tissues where they are effective in controlling plant pests with sucking mouthparts. This sometimes leads to special handling and residue problems and must be treated with caution.

Organophosphorus category: These insecticides are divided into resistance management classes based on the functional groups that are bonded to the phosphorus atom. Once thought to have no equivalent natural toxin in nature, Neumann and Peter (1987) recently reported the isolation and identification of a heterocyclic phosphate from *Streptomyces antibioticus* DSM 1951, that had potent anticholinesterase activity and was equal in insecticidal activity to monocrotophos (Azodrin®).

In general P=S compounds (phosphothionates) require activation to be insecticidal and this occurs rapidly in insects. P=O compounds do not require metabolic activation. Metabolic resistance would be expected to be dependant, in part, on the other groups attached to the phosphorus atom. Because of the potency of their action on cholinesterase, and the difficulty of reactivation of the phosphorylated enzyme, and because of the great amount of structure and activity work done on organophosphorus insecticides, this category is the largest and most diverse group of insecticides (Voss and Neumann, 1992).

Phosphates: monocrotophos (Azodrin®), dicrotophos (Bidrin®). Both of these simple dimethylphosphates have alkyl leaving groups.

Dimethylphosphorothioates: methyl parathion and fenitrothion (Folithion®, Nonathion®) both have aryl leaving groups.

Dimethylphosphorodithioates: azinphosmethyl (Guthion®) and chlorpyrifos (Lorsban®) have an aromatic leaving group and malathion and methidathion (Supracide®) both have alkyl leaving groups.

Diethylphosphorothioates: parathion has an aryl leaving group.

Diethylphosphordithioates: disulfoton (Disyston®) which is a systemic, has a thioalkyl leaving group.

Phosphorodithioate: sulprofos (Bolstar®) with an aryl leaving group has an unusual O-ethyl, S-propyl substitution.

Phosphorothioate: profenofos (Curacron®) is closely related to sulprofos (Bolstar®) with the same O-ethly, S-propyl substitution, but is a P=O compound rather than a P=S.

Phosphonates: EPN is an unusual phenylphosphonothioate with the phenyl group bonded directly to the phosphorus atom, which is unique among the organophosphorus insecticides.

Chlordimeform type: chlordimeform (Galecron®, Fundal®), amitraz (Ovasyn®) and diafenthiuron. These "insecticides" and acaricides have distinct ovicidal activity.

Although chlordimeform registration has been withdrawn, it provided a unique type of control activity in cotton pest control. Known as formamidines in general structure, these compounds have little or no overt topical toxicity. They are widely known to interact with the octopamine receptor in the nervous system, and therefore have a completely unique mode of action, and indeed have a very distinctive structural similarity to octopamine itself. They were suspected of retarding the development of resistance when used with other acutely toxic insecticides, and to have a strongly synergistic effect (Liu and Plapp, 1992).

Diafenthiuron is a new type of octopamine mimic (Kadir and Knowles, 1991). This compound has not been studied fully, nor developed yet, but it is reported to have activities unlike all other insecticides and acaricides except chlordimeform. Since difenthiuron is broken down by oxidation of the thiourea moiety to urea, the parent compound can be thought of as a propesticide. The urea breakdown product appears to have the greater biological activity (Kadir and Knowles, 1991).

Nicotinic type: nicotine, cartap (Caldan®, Sanvex®) and imidacloprid (Confidor®, Gaucho®). The chemical structure of these compounds is based on a natural toxin extracted from marine worms. Cartap is said to interact with the nicotinic acetylcholine receptor at cholinergic synapses in the insect central nervous system. There is a general similarity between the mode of action of cartap and that of nicotine, but little structural similarity between them.

The relatively new compound, imidacloprid (Admire®, Confidor®, Gaucho®) (BAY NTN-33893) is derived from nitromethylene compounds first discovered by Shell Development Company some years ago. Originally, development was delayed due to an instability of the chemicals that appeared to be an inherent property of the chemical structure of the active compounds. The nitromethylenes are also active at the nicotinic cholinergic receptor, and so this category rightly is called a nicotinic type. Nicotinic agents all should inhibit the binding of the specific and highly potent cholinergic ligand, *alpha*-bungarotoxin (Sattelle *et al*., 1989).

Benzoylurea type. These compounds have undergone considerable development in the past few years and continue to be of interest. They are not neurotoxins. Rather they are considered to be growth regulators with the ability to interrupt development. As a result they are relatively slow acting. Despite this, their efficacy has improved so much in the past few years through structure and activity studies, that they rival the most potent neurotoxic insecticides in field efficacy.

Miscellaneous: B.t., *Bacillus thuringiensis* (Berliner). This bacterium produces an endotoxin protein that when ingested selectively disrupts the midgut of certain chewing insects, especially lepidopterous larvae. Although B.t. has been used in crop protection for many years, more recent advances in B.t. technology have improved the strains and pest control products. B.t. is an ideal component in an IPM scheme because, being selective on chewing insects, it is considered completely safe to beneficial insects.

The B.t. endotoxin gene has been bioengineered into cotton plants and insect resistant transgenic cotton are now undergoing field development (Fox, 1992; Ferro, 1993;

Benedict *et al*., 1992; Jenkins *et al*., 1993). Commercial availability on a limited basis is expected for the 1996 growing season.

Resistance to the B.t. endotoxin has already been demonstrated in the diamondback moth, *Plutella xylostella* (Linnaeus) (Tabashnik *et al*., 1990, 1991). The question of the development of resistance in leaf chewing cotton pests to the transgenic plants in commercial development is now being debated (Fischhoff, 1992; Fox, 1992; Ferro, 1993; Marrone and MacIntosh, 1992). On one hand, the expression of the toxin throughout the plant suggests one hundred percent selection pressure, or close to ideal for resistance development which Ferro (1993) predicts will take as few as four generations. The National Audubon Society considers B.t. a valuable resource and is highly concerned that it might be squandered if vigorous attention is not given now to resistance management (Fox, 1992).

The levels and expressions in the transgenic plants are amenable to manipulation and possibly more than one factor may be engineered into the plant to retard the development of resistance more or less in analogy to the use of rotation or mixtures of ordinary insecticides (Fischhoff, 1992). Although some of the transgenic cotton cultivars are spectacular in their protection against chewing insects in the field, at least one recent report (Benedict *et al*., 1992) concluded that a low expression of the endotoxin gene conferred little or no protection compared to control plants.

RESISTANCE MONITORING

Here at last is one area that appears to evoke uniform agreement in the field of insecticide resistance. Everyone agrees that monitoring of resistance is needed (Roush and Miller, 1986; Sawicki, 1987; Riley, 1989). Although there may be some minor disagreements on the details, no one can argue with the spectacular data generated by resistance monitoring of pink bollworm in California, tobacco budworm in Texas and the Mid-South, bollworm in Australia, and green peach aphid in England. For the very first time it has been possible to get good information about the resistance of populations in single fields or in localities.

Preliminary results suggest that resistances to both pink bollworm and tobacco budworm in the United States might even be highly localized. This information is particularly important because the original expectation was that one grower generating a resistant population in one field would cause general problems in a local area.

LESSONS FROM BIOASSAY COMPARISONS

Given that resistance monitoring is widely accepted, one of the first lessons to learn about the subject of insecticide resistance is the folly of relying entirely on one resistance monitoring method. One example of this is in the outstanding work conducted by Tim Dennehy on spider mite resistance in the San Joaquin Valley of California. This work epitomizes what can happen with incomplete testing, and shows the difficulty of distinguishing resistance fact from artifact concerning any particular product.

Reports of failures of dicofol (Kelthane®) to control spider mites of the *Tetranychus* genus, prompted Dennehy, Granett and Leigh (1983) to investigate. They first repeated the standard laboratory test for acaricide efficacy, the well known slide-dip test. The slide-dip test is essentially a topical toxicity assay since mites are dipped in dicofol directly. They obtained a resistance ratio for dicofol of 5.7 comparing field strains of twospotted spider mite, *Tetranychus urticae* Koch, with laboratory susceptible strains.

They then employed a less accepted residue test whereby leaf discs are dipped in dicofol and mites are confined to the treated surface. This residue test gave results that were completely different and showed a 544-fold toxicity difference between susceptible spider mites and field collected mites (Figure 4).

Thus, the Dennehy *et al.* work (Figure 4) shows that reliance on one method, even though widely accepted, may yield misleading results. The other lesson to learn from this classic study is that on close examination, all resistance and field control problems were with the twospotted spider mite. The strawberry spider mite, *Tetranychus turkestani* Ugarov & Nikolski that occupied the same cotton niche was controlled with dicofol (Kelthane®) and showed no resistance.

Schreiber and Knowles (1991) also compared topical toxicity with vial bioassay on the bollworm. They found that the adult vial assay gave results that were similar to adult topical tests, but larval vial assay results were significantly different from larval topical toxicity.

Misleading results with topical assays using standard toxicological testing protocols are not new. Arthur and Zettler (1991) found that topical methods did not accurately reflect malathion resistance frequencies in the red flour beetle, *Tribolium castaneum* (Herbst). Roush and Luttrell (1989) reported that topical bioassays did not accurately detect resistance in the tobacco budworm.

The dichotomy between results of topical bioassay versus residue treatments have also been reflected in improved control by space sprays for house flies compared to residual treatments using a variety of insecticides (Taylor, 1982). These and other examples show the inappropriateness of extrapolating laboratory test results to field situations.

Reliance on a single biochemical test for insecticide resistance is cautioned as being myopic (lacking in foresight) since continuous use of one insecticide may result in the selection of additional mechanisms (Sawicki, 1987). Biochemical tests are sophisticated in that they can often give precise quantitative information on specific metabolic enzymes that play a role in insecticide detoxification such as esterase, or carboxylesterase tests (Devonshire *et al.*, 1986; Hemingway *et al.*, 1986) or cholinesterase tests (Voss, 1980).

Biochemical tests, by their nature, normally are restrictive in what they reveal and cannot substitute for topical or other tests of overall toxicity of insecticides to insects.

RESISTANCE MONITORING METHODS

Attracticide Assay Method — A novel resistance monitoring method was created and perfected for pink bollworm. This method, termed the "attracticide resistance monitoring method", employs Delta traps baited with pheromone gossyplure, that are ordinarily used for assessment of populations of male adult pink bollworms.

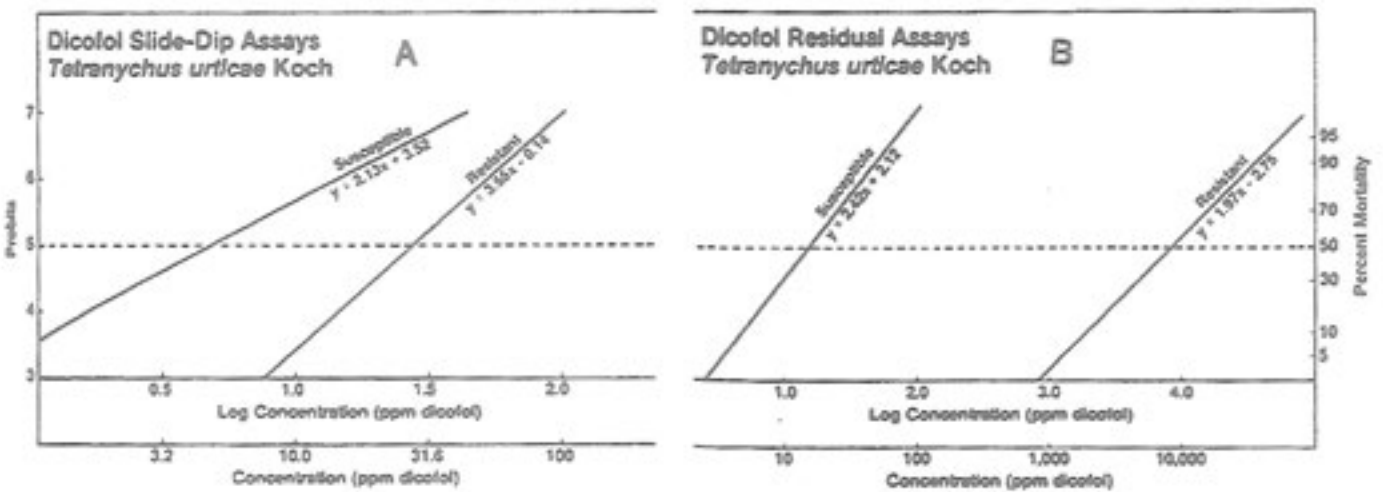

Figure 4. Probit data of dicofol (Kelthane®) on twospotted spider mites collected from cotton fields in central California (From Dennehy *et al.*, 1983). The slide-dip assays (A) and the residual assays (B) gave very different results. The LD_{50} values (horizontal dashed line) between laboratory (susceptible) and field collected (resistant) strains assayed by the residual assay were almost three orders of magnitude different indicating huge resistance to dicofol residues. The topical assay showed a much smaller difference.

To monitor resistance of adult pink bollworm, the Delta trap was purchased without sticky adhesive. Cards trimmed to fit in the bottom of the Delta trap were smeared with a mixture of sticky material (Tangle-Trap®, Tanglefoot Co., Grand Rapids, Michigan) and an insecticide to be tested. Each card had a different concentration of insecticide and a series of three to five concentrations was prepared besides a control without insecticide. The series of doses were replicated for each insecticide at least once.

Modified Delta traps with dosed cards were placed in cotton fields overnight. The traps were collected in the morning before sunrise. The cards with their trapped adult male pink bollworms were removed and stored at room temperature (70F). After two days the number of dead moths and the total number per card were determined. These data together with the mortality of controls for each insecticide were analyzed by probit analysis (See earlier section in this chapter for discussion of probit analysis) program (Raymond, 1986).

Protocols for conducting attracticide tests in the field were described in two papers (Haynes *et al.*, 1986, 1987). It was observed that control mortality was reduced if sticky cards were scraped before use to eliminate blobs of stickum. The attracticide method has been used for pink bollworm resistance monitoring programs in Arizona, Texas, Mexico and China as well as in California.

Data from the laboratory of Dr. Wen-gu Li in Shanghai, China shows the mortality of adult male pink bollworm over time on sticky cards (Figure 5). Similar data on the treatment of third instar tobacco budworm larvae by cypermethrin (Ammo®, Cymbush®) gave remarkably similar results (Firko and Wolfenbarger, 1991) (Figure 6). These results demonstrate clearly the need for a specific incubation period following dosing in order for reliable toxicity values to be obtained. In this case, two days are needed before toxicity data become stable. All studies using bioassay of insecticides require calibration charts such as that of Dr. Li for each species and insecticide category tested.

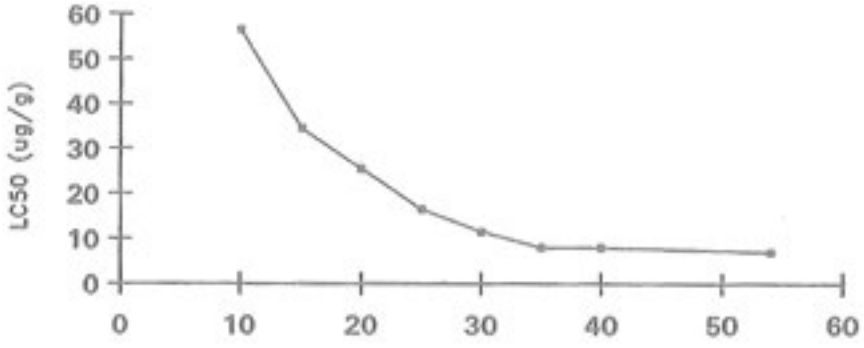

Figure 5. Change in toxicity following attracticide dosing of adult male pink bollworm by fenvalerate (Pydrin®). (From Dr. Wen-gu Li, Shanghai Institute of Entomology, unpublished data, 1991.)

The attracticide method or modifications have been adapted to monitor resistance in codling moth, *Cydia pomonella* (Linnaeus), citrus thrips, leaf miner, whitefly, oriental fruit moth, *Grapholita molesta* (Busck), german cockroach, *Blattella germanica* (Linnaeus) and peach twig borer. Major advantages of the use of insecticide and stickum mixtures are that any formulated insecticide may be used and the mixtures survive cold storage well.

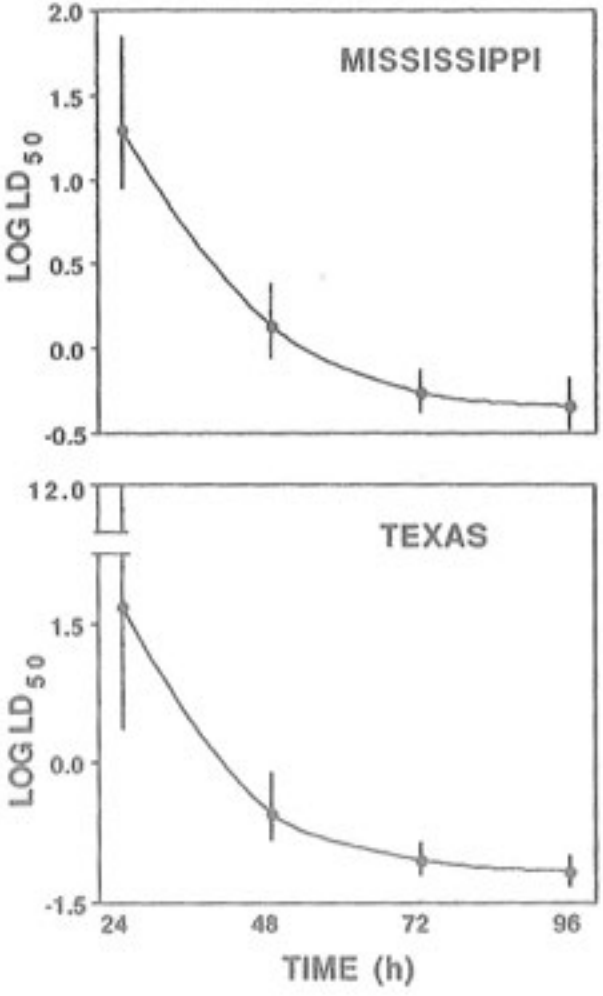

Figure 6. Estimated LD_{50}s (with 95% CI) based on mortality observations 24, 48, 72 and 96 hours after treatment with cypermethrin (Ammo®, Cymbush®) of third instar tobacco budworm larvae from Mississippi and Texas. (From Firko and Wolfenbarger, 1991.)

Vial Residue Assay Method — An alternative method for resistance monitoring was perfected by Plapp (see Plapp *et al.*, 1990; Kanga and Plapp, 1992, and Kanga *et al.*, 1993 for materials and methods). A given amount of insecticide dissolved in solvent is placed in a glass vial (20 ml scintillation vials are perfect for this). The solvent evaporates as the vial is rotated mechanically. When dry, a uniform coating of the insecticide is left on the inside of the vial. Live adult or larval insects are placed in the vial and kept at room temperature usually for 24 hours, before mortality is determined.

Although the vial assay was originally designed for use with tobacco budworm adults as part of a field monitoring program, it is suitable also for testing discriminating doses on adult pink bollworm. The pink bollworm is not nearly so sensitive to temperature in the vial assay as in the attracticide assay method (Schouest and Miller, 1988).

In addition, the vial assay has been adopted for resistance monitoring of the whitefly (Staetz *et al.*, 1992) with one very important modification. It is conducted for only three hours instead of 24 hours as used for pink bollworm and tobacco budworm. The shorter time is needed because there is significant mortality of adult whitefly when held longer than six hours (Figure 7). The immediacy of the whitefly resistance problem is such that the vial assay was adopted quickly despite the obvious drawbacks of assessing mortality after such a short time. This would not reflect fully the metabolic component as demonstrated by Busvine's (1951) results (Table 3) and the von Keyserlingk deltamethrin results (Figure 2). Strictly speaking, the short assay period would make the whitefly results a knockdown assay, not a toxicity or mortality assay, and should be reported as such to avoid confusion.

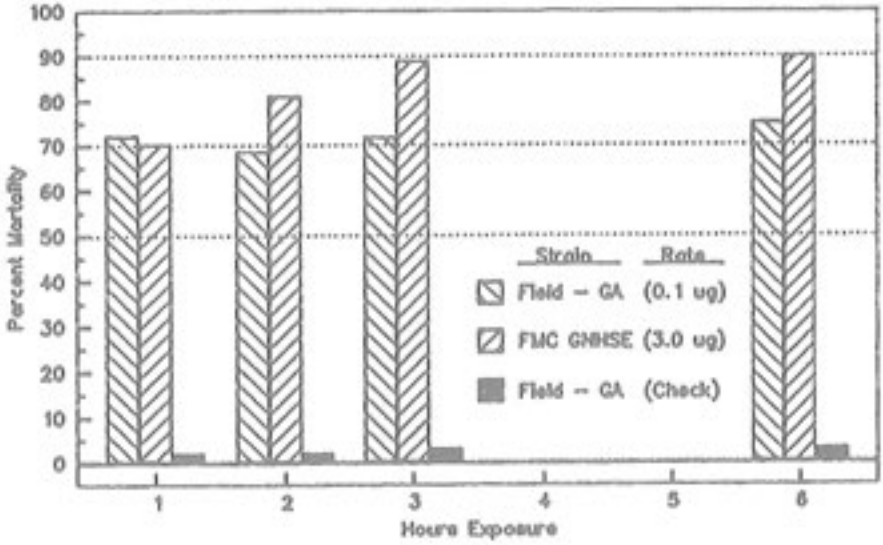

Figure 7. Bifenthrin (Capture®) knockdown of adult whitefly over a six hour period following exposure to treated glass vials. (From Staetz *et al.*, 1992.)

Originally the vial assay was used to monitor only cypermethrin toxicity. Although cypermethrin was selected for a number of sound reasons, no other pyrethroids were monitored. Other categories of carbamate and organophosphorus insecticides were not stable enough on the glass surface to withstand storage or shipment. One way around this would be to make up the vials immediately before use (Personal communication, D. A. Wolfenbarger, USDA, ARS, Weslaco, TX).

Recently, it was learned that organophosphorus insecticides can be adopted for use in the vial assay if care it taken to ensure the stability of the chemical on the glass surface (Kanga *et al*, 1992). If the glass vials are treated with benzoic acid, the insecticide film (residue) deposited on the glass vial becomes far more stable (Figure 8). Still, it

Figure 8. Toxicity of profenofos (Curacron®) to adult house flies confined to glass vials treated with 3 *mg*/vial with or without benzoic acid to stabilize the organophosphate (profenofos). (From Kanga *et al.*, 1993). Note that without the benzoic acid, the toxicity of profenofos drops off rapidly starting immediately after the vials are coated; whereas, with benzoic acid the vials remain effective for bioassay testing for over two weeks.

is a good practice to use organophosphorus insecticide-treated vials quickly, and to be aware of possible degradation upon storage.

FIELD INCUBATION

One of the best methods of saving time during resistance monitoring was to employ on-site incubation. We learned early on that carrying insects from the field to constant temperature chambers for incubation was awkward and time consuming. Yet insects had to be held at constant temperature to insure accurate data and to keep control mortality down to acceptable levels.

Control experiments showed that a hole in the ground maintained a constant temperature sufficient for incubation of field-collected insects (Figure 9). The depth of the hole had to be at least six inches (15.2 cm), but was very stable and convenient at a depth of 28 to 39 inches (70 to 100cm) (Schouest and Miller, 1991).

Data from pink bollworm adults held in the ground in vials, or stuck on attracticide cards was very similar to insects held in environmental chambers with the temperature constantly controlled. This meant that resistance tests could be conducted all on site in rural areas and eliminated the need to carry insects from field collection sites into a laboratory or other special facility.

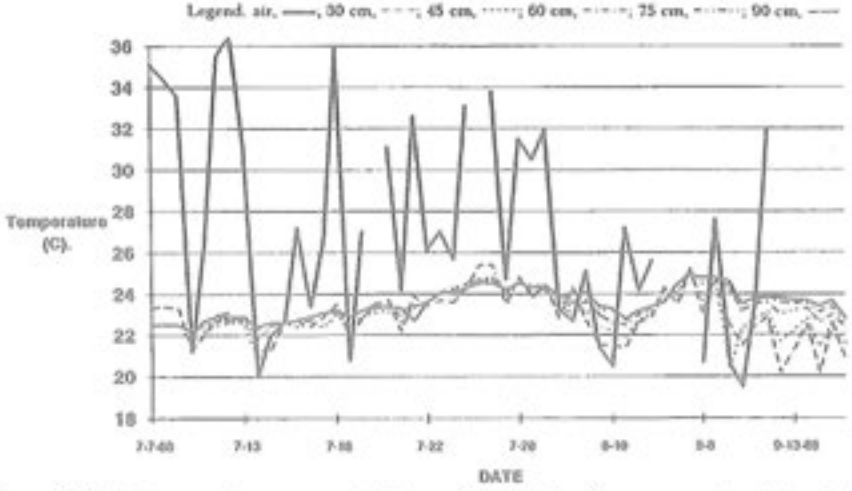

Figure 9. Air temperatures recorded at various depths in a one-meter hole in the ground from July to mid-September at Riverside, California. (From Schouest and Miller, 1991.)

DEVELOPMENT OF RESISTANCE

Resistance management strategies depend on factors that influence the development of insecticide resistance. The list of these conditions is in Table 4 and is modified from Sparks *et al.* (1985).

Insects that just begin to develop resistance show poor viability compared to susceptible strains. Kelly and Watson (1987) confirmed this for laboratory-pressured tobacco budworm. Fitt (1984) reported extensive growth and survival data from strains of *Helicoverpa armigera* that showed this trend. Recently Plapp and his coworkers obtained similar data for the pyrethroid resistance strains of tobacco budworm collected from cotton fields (Table 5).

Table 4. Conditions conducive to rapid development of resistance. (From Sparks *et al.*, 1985.)

1. Prolonged exposure to a single insecticide.
2. Every generation of the insect treated (selected).
3. Selection pressure high (high doses).
4. No insects escape treatment.
5. Large geographic area treated.
6. Selection occurs prior to mating.
7. Insecticide related to one used earlier.
8. Treatment triggered by low numbers of pest insects.
9. Insecticide inherently irritating and/or repellent.
10. No gene flow between insect populations (no migration between populations).
11. Pest insects monophagous (feed mainly on one kind of plant).
12. Short generation time (short life cycle).
13. Numerous offspring per generation.
14. Insects highly mobile.
15. Insecticide has long residue life.

Table 5. Growth, development and reproductive data for susceptible and resistant tobacco budworm males and females. (From Campanhola *et al.*, 1991.)

Characteristics	Susceptible strain		Resistant strain	
	♂ (male)	♀ (female)	♂ (male)	♀ (female)
Mean pupal developmental period, days	15.1	13.5	14.9	13.3
Mean pupal weight, milligrams	324.1	318.8	328.6	315.4
Mortality at pupal stage, percent	1.8	2.4	1.9	2.1
Mean hatching to adult development period, days	31.3	29.8	32.81	31.0[1]

Mean fecundity, number of eggs per female	—	2,552.8	—	1,270.0[1]
Mean fertility (number of females producing eggs), percent	—	93.5	—	62.5[1]
Mean hatchability (hatched eggs), percent	—	74.8	—	71.5
Mean adult longevity, days	21.2	17.4[2]	23.5	14.2[2]
Intrinsic rate of increase, r[3]	—	0.12	—	0.10

[1]Significantly different from the susceptible strain ($P<0.05$; t test).

[2]Mean longevity of females significantly different from males of the same strain ($P<0.05$; t test).

[3]$r = (\log_e R_o)/T$, where R_o is the net replacement rate (number of daughters/female) and T is the mean generation time.

Note: For information on number of individuals tested and statistical confidence limits of results, reader is referred to the paper cited above.

Fitness data are not spectacular because the lack of viability in insects that are just in the process of developing resistance is sometimes a matter of degrees and changes are subtle. Plapp and his co-workers show, for example, that resistant budworm larvae grow more slowly and weigh slightly less than susceptible strains. Adults of resistant strains are less responsive to pheromone than adults of susceptible stains. Females of resistant strains produce less pheromone, lay fewer eggs and have a slightly higher mortality than susceptible strains.

Taken individually, these parameters of growth, development, fecundity and reproduction are not impressive. In fact, some are barely discernable by good statistical comparisons. However, when taken together, they represent a distinct advantage for the susceptible populations providing there is not a continuing selection pressure from the continued use of the same insecticide. If spraying continues, then the selection process continues, swinging the chances of survival decidedly back in favor of the slightly less viable resistant strains.

Muggleton (1984) termed these processes "selective disadvantages," and a few studies have given them quantitative values from 34-56 percent. He concluded that resistance genes have appeared and disappeared spontaneously in all insects and have been doing so all along, certainly prior to the introduction of insecticides.

A recent genetic study of resistance confirmed these trends of fitness disadvantage in the development of resistance (Clarke and McKenzie, 1987). The important feature described by the latter study, however, is that once resistance is selected for several generations, the resistance remains and viability returns. Empirical results confirm this. This explains part of the "rachet up" effect mentioned above which leads to gradually increasing tolerance (the "creep" up of resistance) as insecticide selective pressure is maintained year after year.

Although laboratory selection is said to produce polygenic resistance (Roush and McKenzie, 1987), laboratory colonies under selection sometimes develop an initial resistance followed by reversion to susceptibility for one or two generations before resistance develops (Brown, 1981). Reversion in the field can have two causes: (a) fitness disadvantages to the resistant individuals or (b) dilution of the resistance frequency by susceptible migrants (Personal Communication, R. T. Roush, Cornell University, Ithaca, NY), or reversion of the resistant trait.

Results of laboratory selection may be misleading if inbreeding depression is mistaken for lack of viability (Roush, 1986). Selection in the field will cause inbreeding depression as well if the numbers of insects remaining in any general location is kept low by constant insecticide treatments. Indeed, this is one possible explanation of "selective disadvantage," or reversion.

To understand Condition No. 7 in Table 4, "Insecticides related to one used earlier", one must realize that some similarity exists between the mode of action of pyrethroids and DDT. Both of these categories of insecticides are thought to poison insects by acting on nerve membranes. Although the nature of the interaction may vary with each different chemical in this class, the lethal property of these compounds appears to be their ability to render the nerve membranes permeable to sodium ions over a long period of time. The dissertation work of Vincent Salgado (Salgado *et al.*, 1983a,b) made it clear that neuromuscular blockage could be produced by a prolonged membrane depolarization of only a few millivolts caused by a prolonged increase in sodium permeability.

DDT and the pyrethroids share another property that sets them apart as a class of insecticide. Many members of this group have a negative temperature coefficient of toxicity with some important exceptions. This means that DDT and some pyrethroids are more toxic at lower temperatures and less toxic at higher temperatures. The relationship between temperature and toxicity is a continuous one meaning there is no specific temperature above which DDT is non-toxic.

Furthermore, each insect pest has a different temperature-toxicity relationship with members of this class, and very few of these relationships have been measured and studied. Permethrin (Ambush®, Pounce®), for example, is known to be 10 times less toxic to tobacco budworm larvae at 86F than at 52F (Sparks *et al.*, 1982, 1983; Toth and Sparks, 1988), but fenvalerate (Pydrin®) is equally toxic at the same two temperatures. Because these temperature relationships vary from one species to another, laboratory data may not be a good indicator of field efficacy. Therefore, it is important that field rates are determined empirically.

The pyrethroids and DDT share another property. Both can induce kdr- resistance (knock down resistance) in insects. If kdr-resistance were previously induced by DDT use at some point during the past 40 years, and if some of the genes responsible were still present, then it will be somewhat easier for insects to adapt to pyrethroid sprays by developing kdr-resistance. There is evidence that the budworm resistance to pyrethroids discovered in 1985 includes a kdr-like component (Sparks *et al.*, 1989).

Plans for the management of resistance must take into account the 15 factors listed in Table 4 and also the practices that exist for controlling insects in cotton. As an exam-

ple, the biology of the pink bollworm is described below in relation to the list of factors affecting the development of resistance.

RESISTANCE DEVELOPMENT IN PINK BOLLWORM

Ironically, the current best method of controlling the pink bollworm is use of cultural practices (Bottrell and Adkisson, 1977). A simple early harvest strategy has been shown repeatedly to deny the pink bollworm the time necessary to produce a diapause or overwintering generation. Despite this knowledge and proven strategy, the cotton growers in southern California and Arizona have stubbornly refused to use the short season strategy—at least until 1989, when the Imperial Valley growers finally began to use the strategy.

The pink bollworm, a microlepidopteran, is a selective and endemic infestor of cotton in a circumscribed growing region. Therefore, its presence is much more predictable than other cotton pests. The insistence of the growers in southern desert valleys of the United States on using chemical control has guaranteed the presence and pest status of the pink bollworm for an extended period. This made it the subject of a valuable case study of the onset of resistance to the newly introduced pyrethroid insecticides starting about 1980.

There were several advantages to this study of the pink bollworm over studies of most other cotton pests, except mites and aphids. The pink bollworm was predictable. Its yearly appearance was regular and populations were very large. The pink bollworm pheromone had been described years before and use of pheromone traps was routine which helped to describe and define the population fluxes.

The attracticide monitoring method was created early on. This meant that actual probit values for toxicity could be obtained, instead of the incomplete discriminating dose data that was the hallmark of resistance monitoring of the bollworm and tobacco budworm problems in the Mid-South and Australia. In addition, all insecticide categories could be tested. Resistance monitoring was aimed at adults, the same stage treated commercially. Larval stages were not under selective pressure since they were inaccessible to treatments inside the cotton bolls.

The pink bollworm is a moth in the family Gelechiidae that, in addition to cotton, attacks other plants in the malvaceous group including *Hibiscus* sp. and okra. While they can be found rarely on *Hibiscus* sp., they may be considered essentially monophagous (Condition No. 11 in Table 4) on cotton in the desert valleys of the southwestern United States.

The pink bollworm can have five generations in one year, especially in hot desert conditions (Anonymous, 1984; Noble, 1969; Graham, 1980). Except for early and late season when migration is more likely to occur (Stern, 1979), pink bollworm usually remain in a cotton crop once hostable fruiting bodies or flowers are present. The adults fly a short distance from any given field and thus do not strictly satisfy Condition No. 10, (Table 4) "no migration between populations". However, the total mixing within a field population is relatively low, thus encouraging the development of resistance (Condition No. 10, Table 4).

Yield Loss Due to the Pink Bollworm — Insecticide treatment for pink bollworm can start in June and continue until September. Estimates of the average seasonal cost for chemical control vary between one and three hundred dollars per acre assuming an individual treatment to cost $10 - $15 per acre. Average yield losses to pink bollworm in the Imperial Valley of California for 5-year periods between 1961-1985 are shown in Table 6. After the arrival of the pink bollworm in 1965-1966, the average yield dropped dramatically by more than one bale per acre.

Similarly, the costs for controlling the pink bollworm and pests that arise as a direct result of chemical treatments for pink bollworm were given by Burrows *et al.* (1982). These show a dramatic increase and have remained unacceptably high compared to 1966 and previous years. Unusually high costs for 1977 were due to storms that created a one time climate for explosive insect growth and an inability to get into the field for control measures.

Table 6. Average yield and value of cotton produced in the Imperial Valley of California before and after the arrival of the pink bollworm. (From unpublished data, R. T. Staten, USDA, APHIS Methods Development, Phoenix, AZ.)

Years[1]	Average yield	Average value[2]
	(bales/acre)	($)
1961-65	3.43	1029
1966-70	2.25	675
1971-75	2.13	639
1976-80	2.23	669
1981-85	2.53	760

[1]The pink bollworm was established by 1966.
[2]Based on $0.60 per pound of lint.

Control Methods for Pink Bollworm — Despite the clear success of the technology, there has been spotty acceptance by cotton pruodcers in the use of pheromones—the so-called mating confusion technique—to control the pink bollworm. This method is selective, does not affect other insects, especially beneficials, and fits ideally into a pest management program.

The newer Mitsubishi Rope pheromone technique for pink bollworm control has been studied. Results show that pheromone technology must be applied with care, but can greatly reduce pink bollworm populations when treatments are conducted in large blocks with area cooperation (Natwick and Staten, 1986; Staten, 1987).

The more traditional method of controlling pink bollworm with chemical insecticides is shown in Table 7. This example is at one extreme in that it relies on 12 treatments of one product, the pyrethroid insecticide, Pydrin® (fenvalerate). However, it does illustrate how one can come close to satisfying many of the conditions for rapid development of resistance under existing pest control practices in the desert growing regions.

The field represented in Table 7 has exposed pink bollworm to a single insecticide (Condition No. 1, Table 4). Nearly every generation was selected (Condition No. 2). The commercial dosage (high dose) was used presumably (Condition No. 3). The entire population in this field was treated (Condition No. 4). Treatment was delivered, at least part of the time, before mating (partial Condition No. 6). The pyrethroids are similar in their mode of action to DDT, therefore Condition No. 7 (Table 4) was satisfied. Treatment was probably based on pheromone trap catches thus satisfying Condition No. 8. The pyrethroid insecticides are known to be irritable to most insects pests (Condition No. 9). The commercial compound used, Pydrin® (fenvalerate), is photostable and has a residue life of at least several days in the field, therefore Condition No. 15 was considered satisfied.

The pink bollworm tends to be locally infesting insect in the middle part of the season (Condition No. 10). The pink bollworm, being monophagous on cotton, satisfy Condition No. 11. Five generations per season partially satisfies Condition No. 12. Each female can deposit at least 200 eggs, satisfying Condition No. 13. The adult pink bollworm are highly mobile, satisfying Condition No. 14.

Thus, out of the 15 conditions (Table 4) that are conducive to rapid development of resistance, the field discussed above met, at least in part, 14 of them. Condition No. 5 was the

Table 7. An example of chemical use on a cotton field (144 acres) in the Imperial Valley of California in 1984.

Date		Materials
April	22	Azodrin® + Fertilizer
May	5	Kelthane® + Fertilizer
June	19	Orthene® + Fertilizer + PIX®
	30	Orthene® + Fertilizer + Supracide®
July	6	Guthion® + COTE®
	13	Pydrin®
	18	Pydrin® + Galecron® + COTE®
	21	Pydrin® + COTE®
	23	Pydrin®
	29	Pydrin® + Galecron® + COTE®
August	4	Pydrin®
	8	DEF® + Isobac®
	11	Pydrin®
	16	Pydrin® + Comite®
	22	Pydrin® + PIX®
	28	Pydrin® + Galecron® + COTE®
September	2	Pydrin® + Comite® + COTE®
	10	Pydrin®
	19	Bolstar® + Galecron®

only one that was not met. A treatment schedule as presented in Table 7, is an example of one most likely to produce resistance. Obviously, in a growing area as large as the California Imperial Valley, normal pest control practices will vary from one farm to another. Reliance almost entirely on chemical control has led to extremely high costs (Table 8). The cost of resistance and cost to the environment are not included in the calculation.

It has been learned from resistance monitoring that, especially with pink bollworm, resistance likelihood increases for every year the same plot of ground is planted back to cotton. This is true because pink bollworm overwinters in the same field it infests if it is allowed to diapause in the fall (if cotton in infested areas is allowed to grow past September).

Table 8. Cost for control of Imperial Valley pink bollworm pest complex, 1966 to 1980. (From Burrows *et al.*, 1982.)

Year	Total costs	Total cost/acre	Percent of crop value
	($	($)	(%)
1966	4,219,339	120.33	8.04
1967	5,751,033	168.26	9.99
1968	9,247,736	248.36	12.37
1969	7,250,476	167.06	15.74
1970	22,895,979	651.10	56.64
1971	18,489,124	592.60	51.10
1972	10,853,798	332.94	23.09
1973	13,485,458	363.00	21.17
1974	28,365,110	326.04	26.29
1975	12,517,718	291.11	27.78
1976	10,303,364	153.78	14.15
1977	67,251,863	487.33	79.59
1978	10,060,773	150.16	12.26
1979	15,046,694	156.74	13.27
1980	18,058,080	205.21	16.48

Results of Resistance Monitoring of Pink Bollworm — All results from the first two years of resistance monitoring on pink bollworm confirm what one would expect

from the analysis given above. In fact, one growing area in the Imperial Valley (the area around Westmoreland, Figure 10) appeared from the monitoring data to have sat-

Figure 10. Resistance ratios of fenvalerate (Pydrin®) toxicity measured in the cotton fields indicated on this map of the Imperial Valley, California. The Salton Sea is in the upper left hand corner and the United States-Mexican border is shown by a dot-dashed line. The vertical calibration mark on the left indicates 15 miles or about 24 kilometers. (Tom Miller, unpublished data.)

isfied conditions for development of resistance in 1985 and 1986. The Westmoreland area was known to contain a number of growers who traditionally relied heavily on insecticide spraying, especially pyrethroids, for protecting cotton and they had been complaining of reduced efficacy for some time.

Correlation Between Pink Bollworm Resistance and Insecticide Use — The nature of pink bollworm infestation and the resistance monitoring technique allow plotting the resistance of a specific population of pink bollworm against a given insecticide versus a measure of use of the same insecticide to control the same population of pink bollworms in a given field. Such a plotting was done and is shown as Figure 11. The data show clearly that the more a pyrethroid such as fenvalerate (Pydrin®) was used, the greater the resistance became.

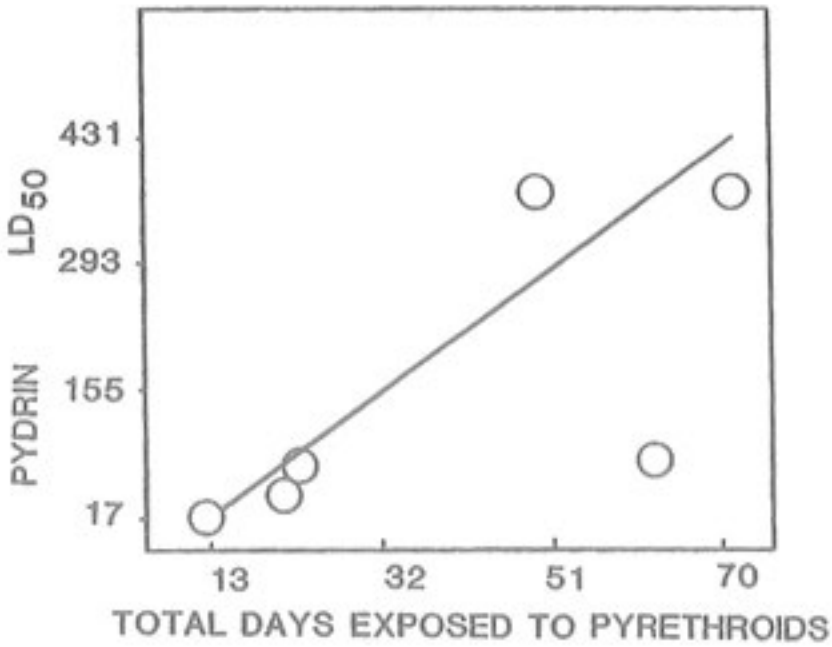

Figure 11. Toxicity of fenvalerate (Pydrin®) to adult pink bollworms plotted against the total number of days Pydrin® was used in a given cotton field. (Tom Miller, unpublished data). All of the data were taken from populations in cotton fields. The cotton fields are shown on the map in Figure 10. As a rule, the longer the population was treated with fenvalerate, the greater the resistance with one exception (the point in the lower right corner). This was from the field with a resistance ratio of 3.91 (on the left side of the map in Figure 10) which was close enough to Mexico to allow an influx of susceptible pink bollworms to dilute the expected resistance.

The Figure 11 plot also shows that resistance was not a discrete increase. Instead, the populations represented showed a gradual increase or "creep" upwards towards greater tolerance in direct proportion to the amount of insecticide used. There is one significant exception, the point in the lower right hand corner of the plot. It represents a cotton field about five miles from the Mexican border. Obviously, the resistance in that field was not proportional to the use of pyrethroid insecticide. In fact, all values of pyrethroid resistance, regardless of its use in controlling pink bollworm, were low near the Mexican border.

We suspected this has happened because pink bollworms tended to bleed across the border at a low but steady extent from Mexico to cotton fields in the United States. Since the Mexican cotton fields were not treated with pyrethroid insecticides at the time these studies were done, they would seem to have served as a source of susceptible pink bollworms to dilute the developing tolerance on the American side of the border.

Mathematicians call this a "boundary effect." As long as conditions of no pyrethroids used in Mexico and extensive use in the American cotton fields are maintained, groups of susceptible populations would be maintained only in American fields close enough to be influenced by the influx of populations from Mexico. The resistance map of Figure 10 gives a fascinating glimpse of how far from the border this influx of susceptible populations penetrated the native pink bollworm populations. Apparently 15 miles was sufficient to negate the effect since resistance was chronically building around Westmoreland.

RESISTANCE DEVELOPMENT IN TOBACCO BUDWORM

Larval stages of insects may have a greater variety of resources to call upon with which to develop resistance compared to adults of the same species because of differences in metabolic requirements in digesting plant material (Brattsten, 1987a,b). The tobacco bollworm, in particular, is more prone to insecticide resistance development than either the pink bollworm or the boll weevil because the larvae stage is accessible to spray treatments, and therefore, is under selective pressure. The pink bollworm and boll weevil are only accessible as adults to commercial spray treatments. The larval stages are encased inside the cotton boll for the balance of their development time and are therefore not under selective pressure.

This generality is important because after the introduction of transgenic cotton plants, presumably the larval stage of the pink bollworm will come under pressure from the B.t. endotoxin for the first time in commercial cotton production. We can only assume that the larval stage of the pink bollworm, like the larvae of the tobacco budworm, will be capable of developing a wider variety of resistance mechanisms than the adult.

Being polyphagous (feeds on many kinds of food), the tobacco budworm has a much stronger mixed function oxidase system with which to overcome toxicants compared to boll weevil or pink bollworm. Therefore it is much more readily able to generate resistive responses to insecticides (Devonshire and Field, 1991; Ronis and Hodgson, 1989). The tobacco budworm is a multihost pest, thereby violating one of the conditions conducive to rapid development of resistance. However, the polyphagous nature of tobacco budworm presents another type of problem when this

pest is treated on cotton then moves to other crops and is treated again, or vice versa. When the same pest is treated on all of its hosts by essentially the same insecticides, then the conditions for the development of resistance are satisfied.

Gene flow studies of tobacco budworm indicate a local population has an average diameter of five miles in mid-season with random mating. Some 13 enzyme loci were studied electrophoretically. Allele frequencies and genotypic proportioning suggested large numbers of insects with high mobility. In conducting these studies, sampling sites were located around the north-western rim of the Gulf of Mexico from south Texas through the middle of the delta states (Louisiana, Arkansas and Mississippi) to one site in Georgia (skipping Alabama) (Korman *et al*., 1993).

One thing still not clear from these genetic studies is why tobacco budworm represents a resistance threat in the United States while bollworm does not (Clower *et al*., 1992; Mallet *et al*., 1993). Both presumably occupy the same niche, and both are treated with insecticides in cotton. Yet traditionally the tobacco budworm has been the greater resistance threat. The answer must lie in the host selection behavior, or details of host preference. This question is in need of further study.

Ironically, the first measurements of resistance in the tobacco budworm to pyrethroid insecticides were conducted on insects collected in the western cotton fields of southern California and in Arizona (Twine and Reynolds, 1980; Martinez-Carrillo and Reynolds, 1983; Kelly and Watson, 1987; Crowder *et al*., 1979; Watson and Kelly, 1991; Unpublished data, J. Leeper, DuPont Chemical Co., Wilmington, Delaware). Despite these measurements of pyrethroid resistance, and the clear warnings and calls for action (Twine and Reynolds, 1980), nothing was done in terms of organizing a concerted effort to develop a resistance management plan until after resistance was apparent.

RESISTANCE DEVELOPMENT IN WHITEFLY AND APHID

Sweetpotato whitefly— named *Bemisia tabaci*, but suspected of existing as a number of strains, perhaps many (Perring *et al*., 1993)—has been referred to as a tropical aphid (Byrne and Bellows, 1991). This designation is most helpful because it lumps aphids and whiteflies together when considering Homoptera in general as cotton pests. This is especially true since aphids and whiteflies are normally kept under good biological control by a number of parasites and predators. As a result, these Homoptera would be prime candidates as insecticide-induced pests, and both are already resistant to a wide variety of insecticides.

The problem is complicated by the fact that whiteflies and aphids contaminate the cotton with honeydew (Toscano *et al*., 1992), and whiteflies pose a virus transmission threat to alternate hosts such as lettuce and melons. This threat is more serious because the result can be loss of entire alternate host crops.

More recently, the B strain of sweetpotato whitefly, or renamed silverleaf whitefly, has been defoliating cotton plants in mid season from Texas to southern California, and including adjacent regions in Mexico. This much more immediate problem transcends resistance problems because of the need for instant control due to the unusual virulence of this strain of the whitefly.

There is abundant evidence that the whitefly has become a pest insect everywhere in the tropics and subtropics. A critical role is assigned to insecticide overuse in this pest emergence (Byrne *et al.*, 1992), and the development of resistance in the whitefly is indicated as being the primary inducement (Dittrich *et al.*, 1985).

Mallet and Luttrell (1991) categorized three types of cotton insect pests. The whitefly and aphid belong to the first category of insect pests which have very high natural rates of population increase (known by ecologists as "r-strategists"), and are capable of readily reinvading a crop once treated. These insects are said to be prone to developing resistance quickly. The use of insecticides exacerbates the increases in population by removing predators and parasites, and increasing rates of reproduction in the pests, thereby increasing the probability of control failure. Experience shows that this type of insect pest tends to be difficult to control with insecticides.

A second category of insect pests may evolve a type of resistance to insecticides that is relatively ineffective, and have a normally low rate of population increase or crop invasion behavior. Boll weevil is considered a good example of this type of insect, and they have been controlled successfully for many years with organophosphorus unsecticides by treating the adult stages.

The third category of insect pests in cotton, according to Mallet and Luttrell's classification, is intermediate between the first two. As long as this pest is susceptible, insecticides control them well; however, as soon as resistance is present in any form, the populations tend to increase more rapidly and the pest response is more similar to the first type of insect pest. The tobacco budworm and bollworm complex is thought to be a good example of this third type of insect with respect to the development of resistance.

Mallet and Luttrell (1991) pointed out that the boll weevil is moved from the second type to the third type of pest insect merely by switching from organophosphorus insecticides to chlorinated hydrocarbons. The adult boll weevil developed resistance to chlorinated hydrocarbons and would, therefore, be prone to have this resistance selected under insecticide treatment pressure. This would lead to population explosions of resistant insects. They concluded, that as a member of the third category of cotton pests, the tobacco budworm is probably the ideal candidate for resistance management approaches.

STRATEGIES FOR INSECTICIDE USE

HOW INSECTICIDE RESISTANCE TRAITS ARE PRODUCED

The theoretical bases for resistance management tactics and strategies all hinge more or less on how the resistance traits are inherited. The question of where resistance genes come from generally has not been addressed.

Natural Mutations — Muggleton (1984) points out that a natural mutation rate is considered to be somewhere around 1 in 100,000 cell divisions. Based merely on the observation that resistance developed fairly rapidly after the postwar introduction and widespread use of organic insecticides, mutations to resistance genes is thought by Muggleton to be a fairly common event. Natural genetic mutations of bacteria are also

thought to be in this same range (Ames, 1989a,b).

Fortunately, there are abundant examples of mutations occurring in the field of medicine. Resistance is a continuing problem with bacteria in hospitals. Indeed, the pathology laboratory of every major hospital operates a routine screening of bacterial samples from patients for resistance to antibiotics. In addition, the treatment of cancer encounters a similar problem in that cells develop resistance to chemotherapeutic agents, and this problem must be dealt with constantly.

New recessive, loss-of-function mutations occur spontaneously in fruit flies at the rate of about 10^{-4} to 10^{-5} per gene per individual, depending on the gene (Strickberger, 1968). Gain-of-function mutations that express a qualitatively new function (neomorphs) generally occur at a much lower rate. The rate is so low, in fact, that it is difficult to measure accurately in fruit flies.

In bacteria, on the other hand, the recessive loss-of-function mutation to arabinose dependence occurs at the rate of 2×10^{-6}, while the dominant, neomorphic, gain-of-function mutation to streptomycin resistance occurs at the rate of 4×10^{-10} (Fristrom and Clegg, 1988). The difference between gain- and loss-of-function mutations is based on mathematical probability. Many different changes in the DNA base sequence of a gene can eliminate its function, but there are far fewer possible ways of producing a new novel function. Classical genetic studies have suggested that the majority of genetically dominant mutations are neomorphs (Park and Horvitz, 1986).

The process of how mutations produce insecticide resistance is not completely understood, but several general points are well established. Insecticide resistance genes often have an altered function, as for example the altered juvenile hormone receptor that produces methoprene (Altosid®) resistance in fruit flies (Wilson and Fabian, 1986), or the alteration of glutathione-S-transferase to catalyze the glutathione-dependent dehydrochlorination of DDT in house flies (Clark and Shamaan, 1984).

Such mutations would be expected to occur at a very low frequency. They would also be expected to show an incompletely dominant pattern of inheritance, and this has been confirmed by genetic studies of many specific insecticide resistance genes (Roush and Daly, 1990; Watson and Kelly, 1991a,b; Payne *et al.*, 1988). This incomplete dominance is of some economic importance, because genetic selection favoring rare dominant (or incompletely dominant) genes is much more effective than selection favoring rare recessive genes (Fristrom and Clegg, 1988). Dominant selection is most effective because all individuals that carry the dominant gene have a selective advantage.

The effectiveness of dominant selection undoubtedly contributes to the difficulty of managing insecticide resistance. One response to this problem has been to treat alternate generations with different insecticides, which should at least reduce the selective advantage of heterozygotes. Another strategy has been to increase the dose of insecticide, to levels theoretically high enough to kill the heterozygotes, so that resistance might become effectively "recessive" (Roush and Daly, 1990). However, this strategy has high economic and environmental costs.

The killing of insects by any insecticide is probalistic rather that all- or-none (even in the laboratory where uniform doses can be applied). An applied dose in the field will

decrease with time (Luttrell *et al.*, 1991) and at the edges of the field, so that some heterozygotes are likely to survive such a treatment and retain a net selective advantage. That is, treatment with insecticides probably always produces selection with some degree of effective genetic dominance (Mallet and Luttrell, 1991).

The apparently very low spontaneous mutation rate to neomorphic mutations (such as DDTase in house flies) may appear to be a minor risk. However, such alleles can accumulate spontaneously over time in unselected populations, so that the natural frequency is much higher than the mutation rate (Fristrom and Clegg, 1988). The extent to which this occurs in insecticide resistance would depend on the selective disadvantage of each resistance trait in the field. This is likely to vary considerably from one type of resistance to the next and is difficult to measure accurately.

The accumulation of rare unselected dominant mutations is best understood in humans. For example, new dominant mutations that cause the human disease called "Huntington's chorea" occur at the rate of about 10^{-7} per individual (actually, this could still be an overestimate, because of the difficulty of proving paternity after the death of the parents). However, the frequency of humans with Huntington's chorea is much greater (about 10^{-4}), so that the vast majority of all individuals with the mutant gene have inherited it from their parents (Hayden, 1981).

Considering the large number of insects per acre, the large number of acres that are treated with insecticides, and the large number of insect generations over which this selection has continued, it becomes clear that the eventual development of neomorphic mutations in localized insect populations is inevitable.

Gene amplification — Insecticide resistance can also be caused by another type of dominant, gain-of-function mutation, known as "gene amplification" (Devonshire and Field, 1991). Gene amplification, also called "hypermorphic mutation" by classical geneticists, refers to the genetic duplication of a normal gene. Multiple copies of a gene, when activated, result in an increased synthesis of the corresponding messenger RNA, an increased synthesis of the corresponding protein, and a net increase in the total enzymatic activity of the protein.

In the green peach aphid, resistance to organophosphates, carbamates and pyrethroids is caused by amplification of the gene encoding the E4 type esterase enzyme; the degree of amplification is about 64-fold (Field *et al.*, 1988). In other strains of resistant aphids, the FE4 type esterase gene is amplified (Devonshire and Field, 1991).

The mechanism of the initial gene duplication mutation is not well understood, although such events are thought to have occurred frequently in evolutionary history (Devonshire and Field, 1991). Also, gene amplification can be reproducible induced by drug selection in cell culture (Schimke, 1986). Genetic duplication events probably occur more frequently than neomorphic mutations.

Once a single gene duplication has become homozygous, subsequent additional duplications occur at a much higher frequency. There are many examples of this in the literature, including resistant aphids (Devonshire and Sawicki, 1979) and cell lines (Schimke, 1986). It is apparently characteristic of gene amplification in general.

Additional gene duplications are thought to occur by a process called "unequal crossing over", which is essentially an normal type of meiotic recombination between duplicated genes. Unequal crossovers occur at the rate of 10^{-3} per duplicated gene per generation in normal humans (Nathans *et al.*, 1986).

The ability of duplicated genes to be repeatedly amplified at a high frequency undoubtedly explains the ability of many resistant insect strains to progressively increase their resistance in every selected generation. This has been shown directly in the case of resistant aphids (Devonshire and Sawicki, 1979), and has been observed during chemotherapy for human cancers.

Treatment of tumors with the cytotoxic drug methotrexate selects for progressive amplification of the gene that encodes dihydrofolate reductase, the target of the drug methotrexate (Schimke, 1986). This results in methotrexate-resistant tumor cells, which many physicians had previously treated by progressively increasing the dose of methotrexate. The strategy was dropped when it was shown to provide an optimal selective pressure for repeated rounds of gene amplification (Schimke, 1986).

Unequal crossing over can produce genetic deletions as well as duplications. By the mechanism of selecting for the deletions, gene amplifications tend naturally to revert to normal at a relatively high frequency. This means that if the selective pressure is removed for a prolonged period of time, insecticide resistance may decline through new spontaneous reversion mutation. This has been reported in aphids (ffrench-Constant *et al.*, 1988a,b; Devonshire and Field, 1991).

Gradually increasing doses of insecticides to counteract gradually increasing resistance as viewed from these mechanisms would probably ensure the accelerated development of resistance. Rotation or other resistance management strategies would have to be employed before any of the insecticides became ineffective.

MIXTURES OF INSECTICIDES VERSUS ROTATION OF INSECTICIDES

The development of resistance to insecticides depends very much on the insect and the insecticide. Rotation of pyrethroid insecticides or acaricides in the Australian and Zimbabwe resistance management strategies respectively was designed to remove one or more generation of pests from selective pressure by a given class of compound. This was also one of the guiding principles behind the Tri-state resistance management scheme; however, the latter suggested, even urged, depending on how one reads the descriptions, the use of mixtures of insecticides, whereas, the former two did not. All three of these strategies/schemes are discussed in an earlier section of this chapter.

Mathematical models of the selective pressure exerted by using mixtures of insecticides rely on modifying the relative fitness values in the fundamental equation of population genetics. Sawicki and Denholm (1987) dismissed such models as being of little practical use because detailed studies of each case were necessary for the best understanding. Others have cautioned that models are exactly that and not meant to replace the much more complex field situation (Tabashnik, 1986; Mallet and Luttrell, 1991). Muggleton (1984) disagreed with Denholm, arguing that such case-by-case studies were themselves impractical because of a lack of resources.

Two studies of the inheritance of insecticide resistance using theoretical models have concluded that mixtures of one or more insecticides are superior to rotation from one category of insecticide to another provided certain conditions are met (Curtis, 1985; Mani, 1985). The models were analyzed using certain assumptions to simplify calculations. Mani (1985) in particular was careful to heavily qualify his conclusions because of these assumptions. He also pointed out that theoretical model studies could provide only a guide to further experiments employing actual field examples, and that resistance management decisions should only come out of practical studies. In this, he appears to support Denholm's conclusion.

One of the assumptions in model studies is that resistance genes are rare. The argument for mixtures of insecticides follows the simple logic that if resistance genes are rare, traits that confer resistance to two different insecticides would be exceptionally rare to occur in the same individual. Indeed, the counter arguments against using mixtures warn that when resistance is already present, even at low frequency, using mixtures would be an inappropriate strategy (MacDonald *et al*., 1983; Wood and Mani, 1981).

The qualifications and conditions for using mixtures were explained and dealt with at length by Mani (1985) who also points out that the choice of chemicals for the mixture has to satisfy various constraints, not the least of which is that the combination should not readily evoke cross-resistance. He cautions, as an example, against combining organophosphates with carbamates because of the chance of evoking an altered cholinesterase resistance that might confer cross-resistance to both classes of insecticides.

For this reason, the description of E4 esterase resistance traits recently described in green peach aphid, *Myzus persicae* (Sulzer), that confer cross- resistance to carbamates, organobosphates and pyrethroids (ffrench-Constant *et al*., 1988a,b) would seem to mute the argument for mixtures of insecticides. Obviously the presence of this resistance gene would outflank a mixture including most of the existing major neurotoxic insecticides currently available for cotton pest control.

There is a danger of placing too great a reliance on theoretical models. Mani (1985) was very careful to point out the need for practical tests in normal field situations. The problem here is one that has nagged resistance management efforts from the beginning; it is difficult to design an experiment that would duplicate or even approach commercial cotton production in such a manner that would account for all of the consequences of insecticide use and give guidance in choosing the best insecticide use strategy.

One particularly troublesome part of the Mani (1985) model is the dose used. "The dosage of insecticide applied is assumed to be large enough to kill all susceptible homozygotes a fraction ... of the heterozygotes ... but no resistant homozygotes." A little reflection and reference to the papers that have been published on this subject (Denholm *et al*., 1983; ffrench-Constant *et al*., 1988a,b; Watson *et al*., 1991) suggests that after an insecticide spray treatment has been made, the residual chemical gradually decreases in amount over a matter of days. This means that once a spray treatment is made, the operator completely loses control of what happens next. In effect, the dose used to treat the insects is changed, not constant (Mallet and Luttrell, 1991).

All too often, thinking about selective insecticide pressure focuses on the single

spray treatment in time and ignores what happens for several days following the treatment. The decreasing dose of a sprayed chemical means that very quickly the conditions imposed by Mani in his model study are changed. For one thing, all of the heterozygotes might very well survive and none of the susceptible insects may survive as suggested by Watson *et al.* (1991) from single treatments by permethrin, particularly if the resistance trait(s) is (are) incompletely dominant, which seems to be commonly the case (Watson and Kelly, 1991a,b; Payne *et al.*, 1988).

The effect of insecticide persistence and mixtures on resistance development was addressed by Luttrell *et al.* (1991) in one of the few studies of this kind. They argued that growers often treat a complex of insects, not just one pest, and tank mixes are therefore, "convenient." Aside from the overall effectiveness of chlordimeform (no longer available to agriculture) in delaying resistance (Liu and Plapp, 1992; Watson *et al.*, 1991), the study found that often two insecticides applied together aged at different rates, leaving one material to act as the selector.

Many side effects of insecticide use are subtle and little understood. Pyrethroid insecticides were known to induce a repellency in insects and mites almost from their introduction (Penman *et al.*, 1986). Repellency affects the overall response of pest insects including those that treatments were not intended to control.

The intriguing side-effect of increasing the reproductive capacity of aphids was documented in response to organophosphorus residues (ffrench-Constant *et al.*, 1988a,b). In addition, Kerns and Gaylor (1991) speculated that somehow sulprofos (Bolstar®) treatments were improving the cotton plant as a host for the cotton aphid leading to population explosions. They noted that cotton plants in sulprofos treated plots continued to grow after the plants in cypermethrin (Ammo®, Cymbush®) treated plots had cut-out. Mathematical models of resistance management fail to take these and other consequences into account. These subtle effects of pest control in cotton would seem to justify Mani's caution.

The observation that cotton aphid susceptibility to insecticides depended on the time of treatment was also intriguing (Grafton-Cardwell, 1991). Instead of just being a change in tolerance, this phenomenon appears to be related at least in part to the physiological state of the aphid itself. Alatiform (winged) nymphs were significantly more tolerant to five insecticides tested compared to apterous (wingless) adults. The phenomenon appeared to be general since the insecticides tested, oxydemeton-methyl (Metasystox-R®), chlorpyrifos (Lorsban®), dicrotophos (Bidrin®), biphenate and endosulfan (Thiodan®), included organophosphorus, pyrethroid and cylcodiene types, each with a distinct mode of action. In addition, survival of treatments appeared to decline as the season progressed, signalling possibly another physiological change in the aphid.

A field evaluation of insecticide rotation versus mixtures for control of citrus thrips, *Scirtothrips citri* (Moulton), found that insecticide rotation was superior in retarding resistance at half the recommended rates of each insecticide (Immaraju *et al.*, 1990). Formetanate (Carzol®), a carbamate, and fluvalinate (Mavrik®), a pyrethroid, were used. In addition, in the absence of selective pressure, fluvalinate resistance regressed to levels before selection after one year.

Tests of mixtures of profenofos (Curacron®) plus cyhalothrin (Karate®) applied at full, half or quarter rates were compared to each compound separately in field plots. Results suggested that the lower rates of the mixtures reduced selection pressure for resistance to both compounds (Kostroun and Plapp, 1992). Thus another qualification for the use of mixtures would urge that they be used only at low rates.

USE OF HIGH VERSUS LOW INSECTICIDE RATES

The use of low rates in the report described above conflicts with the theoretical argument in favor of the use of high rates to control heterozygous hybrid insects with intermediate resistance to insecticides that arise from the first mating of resistance individuals with susceptible insects, the so-called management by "saturation." Again the logic here is deceptively simple. If a resistant adult moth somehow manages to appear in a field population, this individual by itself would not represent a threat, only a potential threat. True to the concept of dilution, if there were sufficient susceptible insects around, the successful mating of two resistant individuals would be unlikely.

If however, the single resistant individual mated with any of the presumed freely available susceptible mates then the off-spring would be heterozygous for resistance. Since most resistances are due to incompletely dominant genes, the heterozygous off-spring would not express the full resistance, but would be somewhat intermediate in response to insecticides. As the logic goes, if a given spray treatment is sufficiently high, it would still be high enough to control the heterozygous resistant individual forcing true resistance to require that two fully resistance individuals mate before a fully resistance survivor could be produced.

Although paraphrased and simplified, the argument given above is essentially the one for high doses as a resistance management tactic (Wood and Mani, 1981). Being theoretically sound, this certainly would work. It might be practical if some way were found to decrease the residual dose of insecticide from full effective rate to zero at some point after spraying.

Perhaps the most pertinent model study of the rate of development of resistance is that of Mallet and Luttrell (1991) who put the subject and interpretation into the context of the cotton industry. They reached some very important, even startling, conclusions making the arguments of rotation of insecticides versus mixtures of insecticides and low versus high doses somewhat academic.

Their first point was that tobacco budworm was not a pest before DDT began to be used for cotton pest control. Indeed, there is little or no use of insecticides in the Central Valley of California and there are no key pests of cotton there outside of occasional mite problems. Perhaps most pertinent of all, the tobacco budworm is present, on alternate hosts, but is not a cotton pest.

Their second point was that many cotton pest insects may not be amenable to insecticide control. In this category they include the cotton aphid and whitefly, both homopterans and both subject to population explosions. Indeed, a number of experiences suggest that spraying causes population increases, not decreases since one negative side effect of spraying is to actually increase the reproductive rate leading to population explosions.

In a useful analysis of the use of low and high doses, Mallet and Luttrell (1991) report that while theoretical analyses are usually based on laboratory data, field dosage-mortality responses are likely to be shallow with genotypes overlapping. Low dose rates would increase heterozygote survival, and high dose rates would eliminate more susceptibles assisted, if anything by shallow dose responses. Either strategy delays resistance, but does not eliminate it. Despite model studies of resistance gene inheritance, in the end, resistance is correlated with insecticide use; the more insecticides are used, the greater will be the probability of developing resistance. Put another way, one cannot develop resistance without using insecticides frequently, i.e., without selective pressure.

NATURAL ELIMINATION OF RESISTANCE

Monitoring the efficacy of a number of insecticides not only tells which compounds show tolerance, it also shows which compounds are still effective, and gives the toxicologist some hint as to the type of tolerance developing. Such monitoring also tends to make resistance management a more natural procedure.

We inadvertently came across natural resistance management operating in the Palo Verde Valley in the spring of 1987. Six insecticides were being surveyed for resistance by the attracticide method at four sites that were selected by Dr. C. A. Beasley of the California Cooperative Extension Service. The tests were conducted by Mr. Richard Wellman, a local commercial pest control advisor. Because of the cost involved, not all compounds were tested at every field. The tests were conducted very early in the season (June 1) before fruiting bodies were present.

The results (Figure 12A) showed that one field (Wuertz) contained a pink bollworm population that showed excessively high tolerance to fenvalerate (Pydrin®). The adults in the Wuertz field were 400-fold more resistant to fenvalerate compared to our susceptible laboratory strain. At the same time all other tests gave results that were considerably lower. Indeed, to even see the various results of the other tests, the data point for fenvalerate at the Wuertz field had to be omitted. When replotted, the results showed a widespread low level resistance to all compounds tested (Figure 12B).

Fortunately, we also tested Cymbush® (cypermethrin) and Guthion® (azinphos-methyl) on the same field at the same time. While the resistance to fenvalerate was high, the same population showed a sensitivity to cypermethrin and azinphos-methyl. This suggested that the resistance to fenvalerate was specific and showed no cross-resistance to another pyrethroid nor to organophosphorus insecticides. Thus the resistance was not likely to be site insensitivity (not kdr-like). The pest control advisor used this information to begin the season using organophosphorus insecticides to control the pink bollworm. When pyrethroids were used a month later, no pyrethroid resistance remained.

The fenvalerate resistance in the Wuertz field was specific to that site. The Chaffin 49 and Chaffin 25 cotton fields nearby showed no such tolerance even though they were within two miles of the Wuertz field. The Wuertz field had been planted to cotton successively for five years. This suggested that pink bollworm populations remained endemic and built up tolerance to the given regime of insecticides, with little gene flow to or from nearby fields.

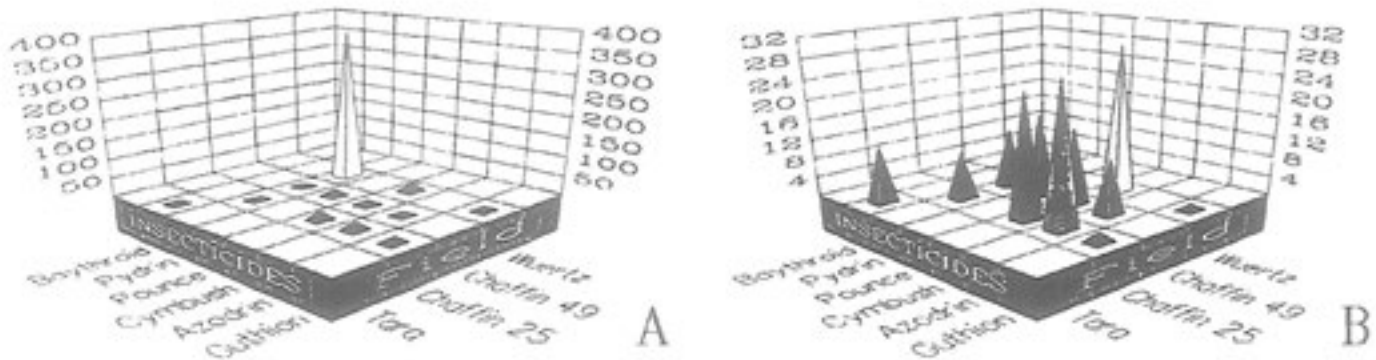

Figure 12. Resistance ratios of six insecticides on adult pink bollworms measured at four cotton fields in the Palo Verde Valley of California in June of 1987 by the attracticide resistance monitoring method. (Tom Miller, unpublished data.) All of the data is shown in A. In B, the large data point from the Wuertz farm was removed to get a better perspective on the remaining values. The Wuertz and Chaffin fields are separated by a few miles in the Valley. The one value of 400-fold resistance to fenvalerate (Pydrin®) was the highest value recorded in field testing. The grower began the season a week later by treating the Wuertz field with organophosphorus insecticides and the fenvalerate resistance was gone a month later. Note the partial cross-resistance to cypermethrin (Cymbush®) at the same Wuertz field, and lack of azinphos-methyl (Guthion®) resistance.

We now suspect that for the past 20 years, following the introduction of pyrethroid insecticides, phenomena, such as that documented in the Wuertz field in 1987, have been widespread. Extensive resistance monitoring in pink bollworm was never established, and the resistance monitoring program was not funded for very long after the development of the attracticide resistance monitoring method.

The commercial pest control advisor, Richard Wellman, who was monitoring the Wuertz field in the spring of 1987, was thinking of switching to organophosphorus insecticides even before the resistance monitoring showed the problem with fenvalerate. He based this "feeling" on the general ineffectiveness of the pyrethroids the previous fall in the same field. Thus insight and practical experience in noticing the efficacy of insecticides in ordinary pest control practices can be as effective as an extensive and expensive resistance monitoring program. The value of resistance monitoring was in establishing exactly what the resistance was immediately and eliminating guesswork in remedying the problem.

SUMMARY AND PERSPECTIVE

The existence of insecticide resistance is now familiar and well established. The factors that confer resistance are generally understood, even if the genetic bases for all of them have not been identified, nor the ecological factors appreciated. The development of resistance to insecticides and acaricides is something that can be dealt with in a rational manner. There are now several successful examples showing that, with a concerted effort, the development of resistance is not nearly as inevitable as once thought.

Fundamental research into the mode of action of insecticides has provided useful tools and information for measuring and understanding insecticide resistance, and designing resistance monitoring protocols. There exists, however, a nationwide trend away from research on insect toxicology. This is occurring at the same time as, but is less well appreciated, the obvious contraction in agrochemical industry. To dismantle the research effort in insect toxicology as one consequence of national concern over the use of pesticides in agriculture, seems neither well thought out nor wise.

One danger in the focus on resistance to insecticides and the effort to seek remedy has been that these approaches and efforts tend to formalize or lock in chemical control methods. Tom Brown touched on this subject over ten years ago (Brown, 1981) when he wrote in the very first paragraph of his review on resistance countermeasures: "In confronting the insecticide resistance problem the most important countermeasure is good pest management practice... to minimize selection pressure from chemical insecticides." More recently, Mallet and Luttrell (1991) reached the same conclusion. The surest way to reduce selection pressure is to use fewer insecticide treatments.

In light of Brown's comment, it is clear why the growers in Texas adopted the short season strategy to circumvent boll weevil and pink bollworm problems very early on, but less clear why the California and Arizona cotton growers on the whole resisted the strategy for years.

It is further remarkable that the cotton growers of California's Imperial Valley, after contending with the pink bollworm as a key pest for some 23 years almost to the point of bankruptcy, finally adopted the short season strategy in 1989. This strategy worked as predicted, quickly relegating the pink bollworm to minor pest status. Several years of insecticide resistance monitoring have revealed that, while valid cases of high resistance to pyrethroid insecticides were found, there were no widespread and obvious failures of insecticides on the same scale found in Texas and Australia in bollworm and tobacco budworm.

This is the main reason why growers in California and Arizona have never pushed for nor sought a resistance management plan or program. In other words, a genuine crisis must occur in order to provoke an effort to actually do something beyond providing token support to a few entomologists in agricultural experiment stations to conduct some measurements. The bigger the crisis, the greater the attention it attracts.

The cultural control of pink bollworm was not the only noninsecticide control tactic available for the past 25 years. Pheromone control applied in the early season now has been shown on several occasions to cause a steady decline in pink bollworm numbers, and has been adopted by a few individual growers. The most common complaint from growers who tried and did not continue with pheromone control was that it worked, but the cost was the same as chemical control. Unmentioned was the fact that pheromone control is so much more compatible with integrated pest management and good resistance management. It is also much less likely that pink bollworms will become resistant to their own pheromone.

Unfortunately, the pheromone system works best to suppress pink bollworm populations when employed over a large contiguous area of cotton. This approach was adopted in California or Arizona in only a few programs because the areawide approach requires cooperation on an unprecedented scale.

Given the will, it is clear that remedial measures preventing or delaying insecticide resistance can be taken. Probably the best that one can expect from a pragmatic standpoint is that resistance management becomes a routine habit rather than something that one reverts to in a crisis atmosphere. How one encourages good integrated pest management, however, is something else.

In 1983, *Helicoverpa armigera* developed resistance to pyrethroid insecticides in Emerald, Australia. The Australians voluntarily instituted a resistance management strategy that has been an integral part of their pest management program ever since. They have supported the monitoring of insecticide resistance and consider that a crucial part of their cotton industry.

The United States had no resistance management program nor plans until 1986 when widespread resistance in tobacco budworms to pyrethroid insecticides appeared at Uvalde, Texas. As a direct result of that incident, Texans began widespread resistance monitoring using the Plapp vial assay method. This method was adopted across the entire southern portion of the Cotton Belt by Arkansas, Louisiana and Mississippi as well as Texas. Monitoring reports have been a common feature of the Annual Cotton Insect Research and Control Conferences in the United States.

Today it is possible to monitor resistance to insecticides not only in the pink bollworm and tobacco budworm, but in almost any pest insect. Such monitoring can be done rapidly and entirely on site in the field, and, in some cases, before the crop is mature enough to be attacked by pests.

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Chapter 10

APPLICATION TECHNOLOGY

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INTRODUCTION

Pest control around the globe has been a problem for many years. The earliest references to the use of a pesticide date back some 3000 years to the writings of the Greeks, Romans and Chinese (Palm *et al*., 1969). The modern use of pesticides in the United States began in 1867, when paris green was used to control outbreaks of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). By the 1920s, the use of pesticides was being accepted more widely in the United States. The development of pesticides expanded rapidly during the 40-year period since the early 1920s. The 1939 discovery in Europe of the insecticidal value of DDT was a revolutionary event for insect control. The use of insecticides on cotton was very instrumental in the establishment of large-scale pesticide applications. In 1986, there were an estimated 14.4 million pounds of insecticides used on cotton; associated chemical costs ranged from 3 to 51 dollars per pound (United States Department of Agriculture, Economic Research Service, 1986).

The application of chemicals with ground equipment began in the early 1900s. This equipment was designed primarily for one person to carry and use. The majority of the pesticide formulations were in the dust form; and accordingly, most of the equipment were dusters. Aerial application of pesticides came into being in 1921 when a load of powdered lead arsenate was dusted on a catalpa grove for control of the catalpa sphinx (Anderson, 1986). Brown (1951) noted that the first aircraft nozzles consisted of pipes extending from a boom and the degree of atomization obtained was not adequate. In 1947, the Mississippi Valley Aircraft Service designed and produced a modern Stearman spray unit (Anderson, 1986). Dusts were still widely used in 1948 but required very favorable atmospheric conditions for sufficient quantities to be effectively deposited. Also in 1948, dust supplies were exhausted by an unprecedented boll weevil, *Anthonomus grandis grandis* Boheman, infestation. Many aerial applicators switched to toxaphene sprays by 1949 (Anderson, 1986). In Texas, only about 5 per-

cent of the treated cotton acreage was sprayed in 1949 (the rest was dusted) but by 1951, over 60 percent of the treated acreage was sprayed. Thus, the research history related to atomization, on-target deposits, drift, contamination and biological effectiveness of sprays is essentially less than 45 years old.

Today, there are many thousands of pest-crop-atomizer-formulation combinations available to producers and crop production personnel. Due to the large number of combinations of possible treatments coupled with a limited resource base, there are obviously many unanswered questions about pesticide applications. Smith (1978) estimated that there were 12.9 engineering scientific years being devoted to all pesticide application problems in the United States and 7.5 scientific years in the Southwest, South and Southeast sections. These estimates included all research on engineering principles as well as research involving all pesticide-pest-crop combinations. With this background and the understanding that the overall application database is incomplete, we will herein attempt to discuss the current state-of-the-art of pesticide application for cotton insect and mite control.

RELATIONSHIPS BETWEEN INSECT/MITE CONTROL AND APPLICATION, FORMULATION, AND/OR METEOROLOGICAL VARIABLES

A partial list of variables which can affect pest control (and yield) is illustrated in Figure 1. Some of these groups of variables such as operational, formulation, deposit on target and nutrients can be altered or controlled. Others, indicating meteorological variables, pest population density, and stage of development and crop foliage structure, must be accepted in their present state for a given temporal (relating to time) period. For purposes of this review, operational variables will include atomizer type, flow rate of the carrier-pesticide mixture, atomizer spacing, boom height, atomizer pressure, and ground speed. In order to further study the effects of "on-target" deposits on insect/mite control, let us attempt to define the target for a crop like cotton.

Some insecticides must be ingested in order to be effective (e.g., bacteria, viruses, protozoa, thiodicarb, [Larvin®], carbaryl [Sevin®]) whereas other insecticides or miticides (e.g., fungi and many chemical pesticides) can cause mortality by contacting an external part of the pest. The contact/consumption mode of pesticide entry can occur over a time period ranging from a few seconds after application until the deposits are washed off or degraded. In addition, any mobile pest may consume or otherwise contact residual deposits on multiple occasions whereas direct impingement on the pest must occur during the application-deposition process. A limited amount of research effort has been devoted to the impingement-residual contact question even though the effectiveness of the two deposition mechanisms is clearly an important issue from the atomization, deposition and safety perspectives.

Scott *et al.* (1974) studied boll weevil control with azinphos-methyl (Guthion®) by both the direct impingement and residual contact mechanisms for sprays applied with

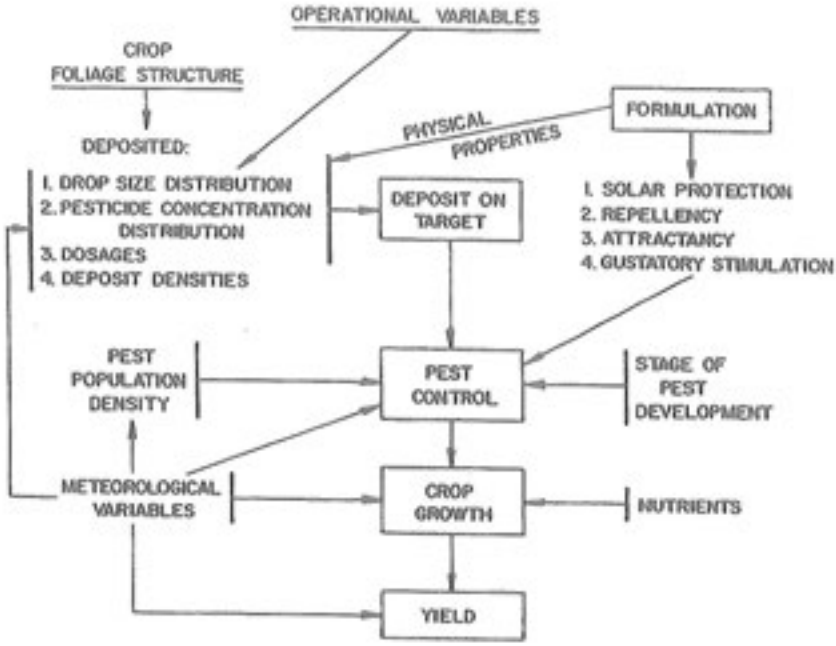

Figure 1. Relationship between application, operational, formulation and meteorological variables on pest control and crop yield.

rotary atomizers (mean droplet diameters between 100-200 micrometers[1]). They reported that the ratio of residual mortality to direct impingement mortality ranged from 1.9:1 to 7.5:1 and the ratio averaged 4.0:1 for all nine treatments. This average ratio indicated that 80 percent of the boll weevils were killed by contacting residual deposits and 20 percent were killed by spray droplets impinging directly on the insect.

Wofford (1985) used cotton terminals mounted in "water pics" to study 'impingement plus residual' versus 'residual' kill of five stages of tobacco budworm, *Heliothis virescens* (Fabricius) larvae sprayed with various droplet sizes and deposit densities (number droplets deposited on target area) for both oil and water carriers. Terminals with larvae on them were sprayed for "impingement plus residual" control and larvae were placed on sprayed terminals about five minutes after spraying for the "residual" control. He reported that the residual mortality accounted for 84 percent of the total mortality observed. Luttrell and Bell (Unpublished data, R. G. Luttrell and M. Bell, Entomology and Plant Pathology Department, Mississippi State University, Mississippi State, Mississippi) conducted a similar test except they released larvae 30 minutes prior to spraying on the upper canopy of whole cotton plants for their

[1]One micrometer (micron) is equivalent to: one millionth (1/1,000,000) of a meter; one thousanth (1/1,000) of a millimeter; and, one twenty five thousand and four hundredths (1/25,400) of an inch. The diameter of a human hair is about 90 microns.

"impingement plus residual" treatment. Their data indicated that for first instars, mortality due to the residual deposits was about 90 percent of the "impingement plus residual" mortality; the percentage progressively decreased to about 46 percent for fifth instars. Their data for first and second instars (i.e., about 90 and 78 percent respectively) are likely representative of field data because young larvae would primarily be located in the upper canopy. MacQuillan *et al.* (1976) directly sprayed native Australian budworm, *Helicoverpa punctigera* (Wallengren), larvae and sprayed tobacco leaf discs to which larvae were exposed. The ratios (LC_{50} data) for the residual to direct impingement mortality ranged from 1.98 to 5.86 and averaged 3.63. The ratio of 3.63 indicates that 78 percent of the larval kill was due to residual activity and 22 percent due to direct impingement.

The three studies with *Helicoverpa/Heliothis* and the one study with boll weevils discussed above indicate that about 80 percent of the control is due to residual deposits. If this trend holds true for other pest-pesticide combinations, then it would appear that the primary deposition target is the plant surface.

For each pest-pesticide-formulation-carrier-crop combination, there are four application related, on-target variables which potentially affect the degree of pest control obtained. These variables are: (a) droplet size, (b) deposit density, (c) dosage (weight of toxicant deposited/area), and (d) concentration of pesticide (weight of toxicant/volume) in the spray. Several studies have been reported relative to the effect of one, two, or three of the four application variables on insect control (Awad and Vinson, 1968; Polles, 1968; Himel, 1969; Burt *et al.*, 1970; Wolfenbarger and McGarr, 1971; Fisher *et al.*, 1974; Smith *et al.*, 1975; Fisher and Menzies, 1976; Jimenez *et al.*, 1976) for various crops-insecticide-insect combinations. These results have indicated that: (a) some larvae can avoid 700 micrometer diameter drops; (b) the predominant droplet size found on boll weevils and bollworm larvae was in the range of 20-40 micrometers; (c) droplets less than about 140 micrometers from ground sprayers will not deposit dependably in or near the treated area; and (d) droplet sizes between 140 and 200 micrometers are reasonable sizes for drift reduction and suppression of both bollworm and boll weevil populations with ground sprayers.

Collectively, these and other studies still leave the applicator in a quandary with respect to how to properly and adequately control insect or mite populations. Other studies have attempted to unify some of the prior data and answer other application questions.

Bioassay type studies have assessed the effect of each of the four application variables (singularly and in all combinations) on insect mortality for both ingestion- and contact-type insecticides (Table 1). The results from six separate experiments indicate that, in every case, dosage was the most important variable. Only in one case (Table 1, bollworm-permethrin-soybean oil) was another application variable nearly equal in relative importance to that of dosage. Collectively, these results indicate again, that the primary objective for an applicator is to get the pesticide onto the target foliage. Secondary considerations appear to be involved when considering the other three application variables (droplet size, deposit density and pesticide spray concentration). The above results (related to Table 1) are all based on bioassay-type tests. However, results from two years

of field studies indicate that the predicted mortalities obtained in bioassays are significantly correlated with several measures of insect control (Luttrell and Smith, 1990).

Table 1. Correlation coefficients or standardized regression coefficients for the four application variables as related to insect mortality on soybean leaves.

Pest - pesticide combination	Application variable			
	Dosage	Droplet size	Deposit density	Concentration
Cabbage looper - *Bacillus thuringiensis* Berliner	0.65[1]	0.34	0.25	0.29
Bollworm - *Baculovirus heliothis*	0.66[1]	0.34	0.47	0.12
Bollworm - permethrin[2]/soybean oil	0.65[1]	0.61	0.20	NS[4]
Bollworm - permethrin[2]/water	0.68[1]	NS[4]	0.19	0.11
Bollworm - fluvalinate[5]/cottonseed oil	0.49[6]	NS[4]	0.07	0.27
Bollworm - fluvalinate[5]/water	0.94[6]	-0.07	-0.24	-0.15

[1]Correlation coefficients from Smith *et al.* (1977a).
[2]Permethrin products include Ambush® and Pounce®.
[3]Standardized regression coefficients from Wofford *et al.* (1987).
[4]Variable would not enter the regression equation due to its small tolerance value.
[5]Fluvalinate products include Mavrik®.
[6]Standardized regression coefficients from Smith and Luttrell (1987).

ADJUVANTS AND BEHAVIORAL MODIFIERS

Insecticides are often applied in conjunction with various materials designed to improve deposition efficiency and/or efficacy. Collectively these materials are referred to as adjuvants, implying that they are usually mixed with insecticides in the spray tank prior to application. However, most insecticide formulations include materials designed to enhance the performance of the active ingredient.

There are many adjuvants designed to perform a diversity of functions. This diversity of materials and functions is extremely complex and beyond the scope of this review on insecticide/miticide application. Popular press articles addressing the advantages and disadvantages of spray adjuvants are common and in some instances (Grondin, 1985) attempt to describe the functions of different adjuvants. This is extremely important since there are many commercial products available for production agriculture. The 1992 Farm Chemical Handbook (Meister, 1992) classifies adjuvants into 23 separate categories based on commercially described functions. Included in these 23 categories are about 225 products or product lines. Often a single adjuvant will be included in several categories (i.e., deposition agent, drift control agent and penetrant, etc.). While the effects of these materials on physical properties of spray mixtures are usually investigated in laboratory studies, effects on field efficacy are difficult to measure and are often

unknown (Grondin, 1985). This lack of experimental data and the complexity of functions associated with adjuvants creates confusion for growers faced with insect control decisions. Recently, Chow *et al.* (1988) attempted to standardize terminology associated with adjuvants and compile available scientific information associated with the performance of adjuvants. Based on their review of the literature, there are more than 1100 scientific papers dealing with various aspects of adjuvants used with pesticide applications. Interested readers should refer to Chow *et al.* (1988) for information on the functions of various adjuvants. Discussion in this chapter is limited to studies associated with the effects of adjuvants on insecticide performance.

In a broad sense, adjuvants affect insecticide performance either by altering spray atomization and/or spray deposit or by altering insect behavior. Spray deposits may be altered before impingement on the target area by changing physical properties of the spray (e.g., changing droplet size distribution, retarding evaporation, and altering viscosity) or after impingement, by changing physical properties of the deposit (e.g., spreaders, wetting agents, and ultraviolet screens). Insect behavior can be altered to enhance the probability of insect contact with the active ingredient (e.g., attractants, feeding stimulants and arrestants). Much of the experimental data associated with the use of adjuvants in insecticide mixtures is associated with microbial insecticides. This is because microbials alone have historically lacked sufficient efficacy to control cotton insects and researchers have sought methods of improving their performance.

EFFECTS OF SPRAY DEPOSITS

A history of adjuvant use with insecticides can be found in Chow *et al.* (1988). During the 1970s, research efforts were made to develop improved formulations of microbial insecticides. Smith and Bouse (1981) reviewed the various factors affecting the application of entomopathogens (pathogens causing insect diseases). The physical effects described would be applicable to all insecticides and are essentially the same as those discussed previously in this chapter. Angus and Luthy (1971) compiled a list of additives used with microbial insecticides prior to 1970. This list includes materials that act as diluents, wetting agents, spreaders, emulsifiers and adhesives. In some cases, adding these materials to unformulated preparations of entomopathogens significantly increased activity. In others, there was no advantage. Angus and Luthy (1971) discussed the importance of using adjuvants with crude preparations of entomopathogens in regard to understanding the physical and environmental factors that limit activity. Most commercial insecticides include in the formulation various materials that alter spray deposits. Smith and Bouse (1981) and Angus and Luthy (1971) advocated more indepth studies on the functions of adjuvants as related to efficacy of entomopathogens. The literature is essentially void of sound scientific data that relate physical properties of spray deposits to insecticide efficacy. Some of the earlier discussion associated with spray deposit studies (Wofford *et al.*, 1987 and Smith and Luttrell, 1987) indicates the general lack of information on these relationships.

During the 1980s, interest in using vegetable oils as a carrier for insecticide applied at reduced volumes stimulated additional research. Several researchers (McDaniel,

1982; McDaniel and Dunbar, 1982; Clower *et al.*, 1982; Luttrell and Wofford, 1984; Luttrell, 1985; Hatfield *et al.*, 1984; Robinson *et al.*, 1986) reported that reduced volume applications in vegetable oil controlled *Helicoverpa/Heliothis* on cotton as well as higher volume applications in water. Similar findings in studies with the boll weevil were reported by Treacy *et al.* (1986) and Wolfenbarger and Guerra (1986). In some of these studies, a slight trend for increased insect control was observed with the reduced-volume, vegetable oil, application technique. However, the exact reasons for the trend were poorly defined and any increased control was not consistent enough to justify the additional cost for the carrier.

Reducing the volume and simultaneously changing the carrier affects the characteristics of the deposited spray (Smith and Bouse, 1981). Hatfield and McDaniel (1984) and Luttrell (1985) measured differences in deposit characteristics between the two application techniques. McDaniel *et al.* (1983) concluded that the trend in increased performance with the reduced-volume, vegetable oil treatments was associated with a more uniform deposition of spray across the spray swath. Slight differences in insect mortality observed in laboratory studies (Luttrell and Wofford, 1984) would suggest that other factors may also be involved. Wolfenbarger and Guerra (1986) suggest that the vegetable oil may enhance movement of pyrethroid insecticides through the insect's cuticle. Reduced-volume applications of insecticides in vegetable oil most certainly alter the physical properties of the spray deposit, but the relative importance of these changes in regard to overall performance of the insecticide is unknown. Most of the studies conducted with the reduced volume-vegetable oil techniques had many variables confounded in the experimental design. Also, most of the studies were direct comparisons between two application methods and were not specifically designed to describe the mechanisms involved. In most cases, dosage (actual amount of active ingredient deposited per unit of area) was not directly measured. Thus, it is difficult to separate treatment differences due to deposition efficiency and deposit characteristics following impingement. Furthermore, since vegetable oils may act as feeding stimulants (Daum *et al.*, 1967), it is difficult to separate effects of these application methods on deposit characteristics from effects on insect behavior.

Until research is conducted that will accurately relate the effects of spray deposits to insecticide performance, the confusion over the value of spray adjuvants will continue. Studies which include measurements of the physical properties of the spray deposit and quantitative indices of insect behavior, both relative to overall efficacy, are essential if we are to understand the role of adjuvants in the application process.

EFFECTS OF BEHAVIORAL MODIFIERS

The use of baits in insect control has a long history. In cotton insect control, the development of a bait which acted as an attractant and a feeding stimulant for boll weevils (Daum *et al.*, 1967) stimulated research with adjuvants as behavioral modifiers. Since most microbial insecticides must be consumed to be active, the bait principle had a logical appeal to researchers interested in improving the efficacy of microbial insecticides.

McLaughlin (1967) used a cottonseed based material as a feeding stimulant in studies conducted to evaluate the effectiveness of a protozoan for boll weevil control. This same bait was modified and included in numerous studies [Bell and Kanavel, 1978; Bell and Romine, 1980; Luttrell *et al.*, 1982a,b; Luttrell *et al.*, 1983; Smith and Hostetter, 1982; Smith *et al.*, 1982b; and prior research reviewed by Bull (1978)] to identify materials which would improve the efficacy of microbial insecticides for *Helicoverpa*/*Heliothis* spp. control. In general, the cottonseed based adjuvants and some soybean based adjuvants (Smith *et al.*, 1981) increased the efficacy of the microbial insecticides. The increase was generally not enough to make microbials perform as well as chemical insecticides. As with studies associated with adjuvant affects on spray deposits, the exact mechanisms involved in increased performance were difficult to measure. Ignoffo *et al.* (1976) reported that a spray adjuvant commonly described as a bait may actually function as a sunlight protectant and an evaporation retardant, as well as a gustatory (relating to the sense of taste) stimulant. Most of the literature associated with the use of baits in applications of microbial insecticides was reviewed by Bull (1978).

Semiochemicals, such as pheromones, have also been tested as possible components in insecticide sprays. These materials offer potential as control agents alone (Mitchell, 1981), but their appeal as an attractant for insecticides is of contemporary interest among entomologists. There has been some interest and success in using pheromones with insecticides targeted against adult insects such as the pink bollworm and the boll weevil. McKibben *et al.* (1990) recently developed an attract-and-kill device for boll weevils that has considerable promise in managing field populations. Although experimental data are lacking, increased research on the role of semiochemicals in insecticide formulations is likely. Some commercial products (Meister, 1992) that include behavioral modifying components in the formulation are appearing on the market.

Overall, the role of adjuvants in cotton insect control is poorly understood. Previous research has shown that adjuvants can alter spray deposits and alter insect behavior. With societal concern for reducing insecticide usage, increased research on the role of adjuvants for improving efficacy is needed. These studies should emphasize an understanding of the mechanisms involved, both from the perspective of the degree of spray atomization and the resulting spray deposit and from the perspective of altered insect behavior. Smith and Bouse (1981) suggested that researchers should consider innovative delivery systems for microbial insecticides. Transgenic plants that express the endotoxin of *Bacillus thuringiensis* is an example of an innovative insecticide delivery system.

APPLICATION OF MICROBIAL INSECTICIDES

In Europe, Aristotle was the first to mention that bees suffered from a disease and, in 1835, Agnostino Bassi discovered the fungus *Beauveria bassiana* as the causal agent (Burges and Hussey, 1971). They further stated that the first commercial microbial product in the United States (which contained *Bacillus thuringensis*) was produced before 1938. There have been several hundred bacteria, viruses, fungi and

protozoa discovered and researched to some degree for possible use as an insecticide. The two groups which have received the most research emphasis for cotton insects are the bacteria and viruses.

The application of microbial insecticides for a wide range of crops, meteorological conditions, formulations and equipment (aerial and ground) has been reviewed by Smith and Bouse (1981). They concluded that on-target spray droplets in the range of 100-150 micrometers provided better insect control than larger drops when the on-target dosages were equal. They also emphasized that much of the "application" research in the literature involves a comparison of equipment types and/or formulations where insect control or yield was used as the independent variable, but typically there were few or no deposit measurements made. The absence of such data negates the possibility of answering the question, "Why was this piece of equipment or formulation better than another one?". Such answers are basic for the development of reliable, functional application systems. The above problem (related to the absence of adequate data) is not restricted to microbial applications but is also prevalent for chemical insecticide applications.

Many cotton insect control studies have involved evaluations of one or more microbial insecticides and/or formulations. In such tests, a chemical insecticide was often included as a reference treatment. Based on both field and field-plot tests, the current general recommendation and practice is to use a microbial insecticide (if one is used) in the early part of the cotton growing season (i.e., when pest populations are normally low) to minimize any detrimental effects on the predator and parasite populations present. The appropriate equipment and operating conditions for such applications currently have not been shown to be any different than those used to apply chemical insecticides. A list of some of the equipment and operating conditions for use with chemical insecticides or miticides are discussed in the next section of this chapter.

APPLICATION OF CHEMICAL INSECTICIDES AND MITICIDES

Several documents are available to assist applicators and others with the selection and proper use of spray equipment. These include multi-topic manuals such as those by Akesson and Yates (1974), Colvin and Turner (1976), Anonymous (1976), Shanklin and Tucker (1980), Hughes (1982) and O'Neal and Brazelton (1984). Other manuals deal with specific topics such as calibration (Rester, 1982) and spray drift (Ware *et al.*, 1983; Smith *et al.*, 1993). Also, many other brochures and manuals have been published by various divisions, departments or universities within each state. Due to the availability of this type of information, we will not attempt to include a synopsis of the same material here.

In a prior section of this chapter, the literature with respect to application variables—as they are presently understood to be related to insect, and possibly, mite control—is reviewed. This section summarizes some of the application equipment-operating conditions-carrier types which have provided effective insect or mite control or produced a droplet size distribution similar to treatments which have been effective.

Similar droplet size distributions should produce similar deposited dosages (for a given carrier) and the prior information in this chapter indicated that dosage was usually much more important than: (a) droplet size, deposit density and spray concentration (the three deposit related variables), and (b) the amount of insecticide impinged directly on larvae. The reader should be aware that the equipment-operating conditions-carrier type recommendations listed subsequently involve subjective decisions because every pesticide application will yield some degree of pest control. However, we have attempted to include only those combinations likely to cause a high degree of pest control under field conditions. These lists of "effective treatments" should not be considered as all-inclusive because there are an unwieldy number of combinations of atomizer types and sizes, aircraft speeds, atomizer orientations, carriers and liquid flow rates which will produce droplet size distributions within a given range. Also, many application related papers/reports have not included adequate information — information concerning one or more of the variables known to affect the degree of atomization — to be used herein. The omission of important application information is unfortunate because there are many good pest control data sets and excellent pest control is the primary objective for crop protection operations. For example, all of the suggested treatments in Table 2 for aerial applications are based on either atomization or deposition criteria, whereas most of the ground treatments are based on insect or mite control data. The lists (Table 2) should provide a selection of useful treatments per se and provide guidelines for selection of appropriate future treatments which are not listed. In addition, a computer spreadsheet has been developed to assist aerial application personnel with the selection of equipment and operating conditions which will produce a desired volume median diameter and a desired number of gallons applied per acre (Smith *et al.*, 1992).

Table 2. Equipment and operating conditions which have been judged to provide satisfactory insect or mite control under most application conditions when using oil[1], water or oil-water carriers.

Equipment and operating conditions						
Atomizer or Nozzle	Pressure (psi)	Nozzle[2] Orientation (degrees)	Speed (mph)	Size[3] (mm)	Pesticide criteria code[4]	Reference
			Aerial - Water			
D4	40	135	90	—	D	Nelson & Lincoln (1968)
D6	40	135	90	—	D	Nelson & Lincoln (1968)
D6	40	90	100	—	A	Yates *et al.* (1985)
D7	60	135	90	—	D	Nelson & Lincoln (1968)
D8	35-55	135	90	—	D	Nelson & Lincoln (1968)
D4-45	40	0	50	—	A	Yates *et al.* (1985)
D4-46	40	0	100	—	A	Yates *et al.* (1985)
D4-46	40	90	50	—	A	Yates *et al.* (1985)

D6-45	40	0	100	—	A	Yates *et al.* (1985)
D6-46	40	90	100	—	A	Yates *et al.* (1985)
D7-46	21	90	100	—	D	Ware *et al.* (1984)
D8-45	45	90	80	—	D	Brazzel *et al.* (1968)
D8-46	40	90	100	—	A	Yates *et al.* (1985)
B10-3	30	0	130	—	D	Southwick *et al.* (1986)
8004	40	0	100	—	A	Yates *et al.* (1982)
			Aerial - Oil			
8002	30	120	100	—	A	Bouse & Carlton (1983)
8002	30	120	120	—	A	Bouse & Carlton (1983)
8002E	35	90	130	—	D	Southwick *et al.* (1986)
8002E	30	120	120	—	A	Bouse & Carlton (1983)
Micronair				165	D	McDaniel *et al.* (1983)
Micronair		40 (blades)	80	—	D	Brazzel *et al.* (1968)
D2-23	18	90	115	—	A	Hatfield *et al.* (1984)
			Ground - Water			
Spinning disc				190	I	Robinson *et al.* (1986)
TX-6 cone	40			—	D	Ware *et al.* (1975)
TX-6 cone	60			—	I	Herzog *et al.* (1983)
TX-6 cone	65			—	I	Hopkins *et al.* (1979)
Raindrop/ D3-23	50			—	I	Hopkins *et al.* (1979)
8001LP fan	20			—	I	Hopkins *et al.* (1979)
Electrostatic				40 (-4 mA charge)	I	Herzog *et al.* (1983)
			Ground - Oil			
Spinning disc				100-140	I	Burt *et al.* (1970)
Spinning disc				100-120-150	I	Smith *et al.* (1973)
Spinning disc				80-190	I	Robinson *et al.* (1986)
Micromax (3500 rpm)				—	I	Treacy *et al.* (1986)
			Ground - Oil/Water			
Spinning disc				190	I	Robinson *et al.* (1986)
Mixcromax (3500 rpm)				—	I	Treacy *et al.* (1986)

[1]For research conducted between 1960-79, the oils were usually petroleum derivatives whereas in the 1980s, the oils were usually plant-derived products.

[2]For aerial sprays, a zero-degree orientation angle indicates that the liquid was sprayed straight back; 90 degrees indicates straight down; etc.

[3]Particle size is expressed as micrometers (mm) for volume median diameter (VMD). VMD is the size for which half of the particles is larger than the VMD and half from particles smaller than the VMD.

[4]Selections based primarily on deposit (D), insect or mite control (I), or atomization (A) considerations. Atomization guidelines for aerial sprays were volume median diameters of 275-350 micrometers for water sprays and 150-225 micrometers for oil diluants.

DEPOSITION EFFICIENCY

As indicated previously in this chapter, most of the early cotton insecticides were manufactured in the dust form and were applied with either ground or aerial dusting equipment. The change from dust to spray applications in either the suspension or solution form, was fortunate from an application perspective because sprays generally have a better deposition efficiency than dusts. The small size of dust particles causes them to decrease in velocity very rapidly and thus deposit very inefficiently on plant surfaces.

The terminal velocities for various sizes of droplets or particles and their corresponding predicted deposition efficiencies (Figure 2) are based on corresponding equations and data presented by Orr (1966) and Miles *et al.* (1975). The terminal velocity is the maximum speed which a given size particle or droplet will attain when freely falling. The deposition efficiencies were estimated for particles or droplets within a plant canopy (i.e., zone of low wind velocities due to the presence of a plant canopy). We used a droplet or particle velocity of 2 feet per second (0.61 meters per second) to calculate the deposition efficiencies. The characteristic target size was 0.25 inch (0.6 centimeter) which could represent parts of squares, small leaves, stems or small trajectory angles for droplets approaching larger leaves.

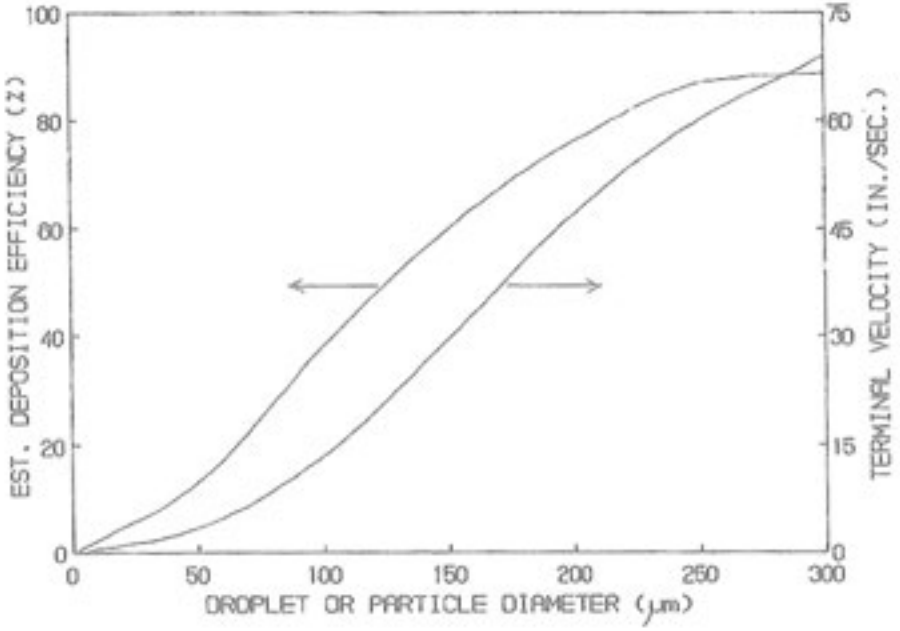

Figure 2. Estimated deposition efficiencies and the associated terminal velocities for spray droplet sizes normally used for insect and mite control.

The reason why small (i.e. less than 50 micrometers) droplets or particles do not typically deposit efficiently on cotton plants or other targets is illustrated in Figure 2. For example, the terminal velocities of 10, 50, 100 and 200 micrometer droplets or particles with specific gravities near 1.0 (i.e., specific gravity for water) are 0.24, 4.0, 13.5 and 47.0 inches per second, respectively. The corresponding estimates for deposition efficiencies are 1, 12, 34 and 76 percent. Thus the larger droplets possess the mass and velocity needed to effectively hit a plant surface. The results of Latta *et al.* (1947) and Miles *et al.* (1975) are in reasonable agreement for droplet or particle size of about 80 micrometers. Akesson and Yates (1974) listed particle size data for several clay dusts. Their data, as well as other sources, indicate that nearly all of the particles were less than 75 micrometers with the majority being less than 20 micrometers. The volume median diameter (VMD, size for half of the volume is from particles larger than the VMD and half from particles smaller than the VMD) for typical dusts would thus range between 15 and 50 micrometers. By comparison, typical spray droplet size distributions for cotton insect or mite control range from a few micrometers up to about 300-400 micrometers with volume median diameters between 100 and 200 micrometers for ground sprayers and 150 to 300 micrometers for oil and water sprays applied by air.

Bowen *et al.* (1952) ran several field tests and found that the deposition efficiencies on bean leaves for charged and uncharged lead arsenate dusts were 23 and 10 percent, respectively. Results reported by Bache and Uk (1975) indicated that the deposition of droplets greater than 40 micrometers in diameter on cotton was predominately by sedimentation rather than impaction. Both of these data sets are supportive of the wind tunnel and theoretical data reported by Miles *et al.* (1975) and the relationships illustrated in Figure 2.

Data from field tests with various sizes of droplets have indicated that droplets smaller than about 100 micrometers initially (larger for aerial sprays) will not be deposited dependably in the swath area unless forces other than gravitational forces are used (Smith *et al.*, 1975). Mist blowers or other types of high velocity air streams have been evaluated in an attempt to control the placement of the smaller droplets. Generally, such approaches have not been more effective than conventional ultra low volume (ULV) or low volume (LV) treatments for cotton insect or mite control (Wilkes, 1961; Burt *et al.*, 1966; Taft and Hopkins, 1967; Taft *et al.*, 1969). One exception to the above generalization was reported by Johnstone *et al.* (1977). They used droplets of about 60 micrometers entrained in an airstream and apparently released the droplets close to cotton plants. For their conditions, they accounted for 94 percent of the spray within 49 feet downwind. They estimated that the drift loss was about 5.5 percent. Small droplets (about 40 micrometers) have also been electrostatically charged to improve the magnitude of deposits on plant surfaces (Law and Bowen, 1966; Splinter, 1968; McCartney and Woodhead, 1983). Herzog *et al.* (1983) reported that cotton insect control for such a spray was superior to that obtained with a sprayer equipped with TX-6 cone nozzles if the charging system was functioning properly.

The knowledge base for the efficient deposition of the smaller, drift-prone droplets has improved substantially in the past ten to fifteen years but much engineering and safety work remains before such systems can be recommended for applicator use.

One would not realistically expect the deposits on the upper parts of a cotton canopy to be as large as the calibrated application rate for several reasons. The calibrated application rate (i.e., either the amount of pesticide or the volume of spray) is based on the land area involved whereas the deposited amount of spray is based on the surface area of a specific target on the plant. In the upper canopy, the wind often alters the orientation of leaves. The leaf may be inclined at some angle or even temporarily curled back over itself during applications. In such situations, the deposit area of the target can be substantially reduced relative to the surface area of the target. This means that the "spray cloud" was directed toward a smaller area than was used to calculate the magnitude of the deposits. Another reason why actual deposits are typically smaller than the calibrated amounts is that the spray droplets do not all approach a given target at the same angle. Miles *et al*. (1975) calculated the approach angles (referenced from the vertical plane) of various size droplets in a 2-feet-per-second air stream. Their approach angles for 20, 100 and 200 micrometers diameter droplets were 89, 67 and 49 degrees, respectively. The large approach angles (i.e., nearly horizontal trajectories for droplets less than 50 micrometers) reduce the effective deposit area of a horizontally oriented target and thus reduce the amount of pesticide deposited per unit of surface area. For example, interest in electrostatic charging of dusts and sprays was based on using electrostatic forces to draw the small droplets or particles toward a plant surface and thus increase the effective deposit area.

Another research area of particular importance is the proportion of spray material recovered at the target. We found only eight published papers/ reports on aerial-water sprays which were sufficiently complete with respect to the application equipment and operating conditions, so that a graph of percent recovery versus volume median diameter of the originating droplet size distribution could be developed. In some cases, we used the author's description of the atomizers and operating conditions to estimate the volume median diameter based on other published atomization data. Because some of the droplet size data were estimated by the present authors, the reader should be aware that the data are not likely to be totally accurate. However, our estimated volume median diameter data should be correct to within plus or minus 20 percent. The on-target recovery (Figure 3) on upper cotton leaves and inert targets increased from approximately 20 to 80 plus percent for volume median diameter droplet sizes of 150 to 1200 micrometers when using water as the carrier. Other than one high and one low set of data for volume median diameters between 300 and 400 micrometers, the rest of the data formed a reasonably well-defined relationship. For volume median diameters between about 90 and 800 micrometers, the variation in percent recovery for a given droplet size is on the order of ±10 percent. Because the recovery data ranged from about 20 to 60 percent of the amount applied for volume median diameters less than 800 micrometers, plus or minus 10 percent represents a substantial, but apparently real, amount of variation in pesticide deposits. The volume median diameters between 500

and 1300 micrometers (Boving and Winterfield, 1980) are larger than would typically be used for cotton insect control but are in general agreement with the recovery-volume median diameter data for volume median diameters less than 500 micrometers.

The data in Figure 3 raise some important questions related to aerial application of water-based sprays for insect or mite control. For example, if the volume median diameter is increased to, say, 500 or 600 micrometers, will the deposits on cotton plants increase? If the deposits do increase, will insect or mite control also be improved? Polles (1968) stated that tobacco budworm larvae could avoid deposited droplets as large as 700 micrometers. However, for a typical 500, 600, or 700 micrometer volume median diameter spray, one half of the spray volume would initially (prior to evaporation) be in droplets less than or equal to 500, 600, or 700 micrometers. Therefore, will the trade-off between possible increased deposits and reduced deposit densities or adverse insect behavior have a positive effect on insect or mite control?

The maximum size droplet which will adhere to a given target is a function of the physical properties of the target and liquid, the size and velocity of the droplet and the orientation of the target. It is not surprising that the magnitude of spray recoveries is quite variable because there are many uncontrolled variables which affect the deposi-

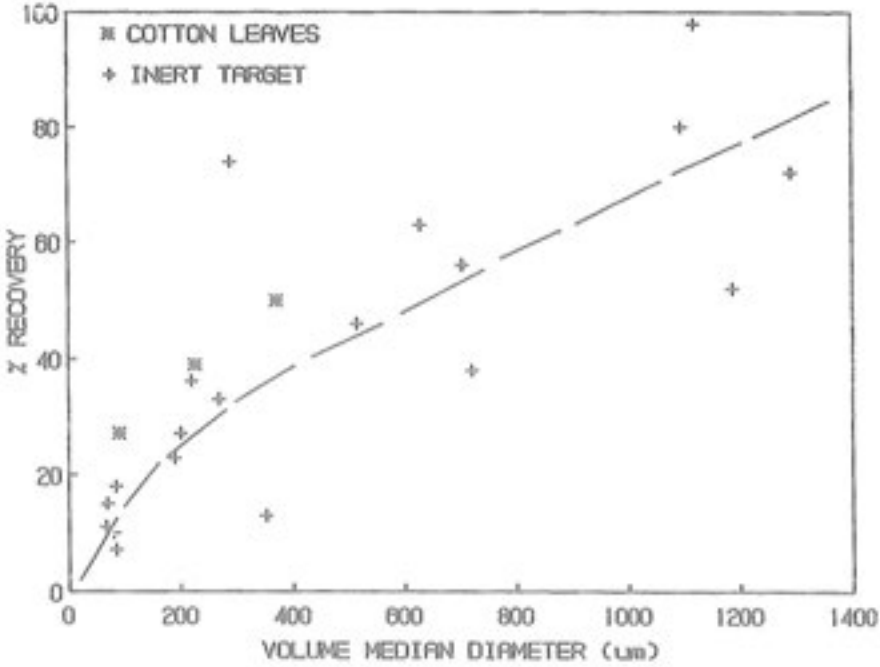

Figure 3. Percent swath recovery versus droplet volume median diameter for aerial sprays with a water carrier from results reported by Brazzel *et al.* (1968), Boving and Winterfield (1980), Uk and Courshee (1982), McDaniel *et al.* (1983), Potter (1983), Ware *et al.* (1984), Sanderson *et al.* (1986) and Southwick *et al.* (1986).

tion process. The largest volume median diameter sprays we found where deposits on cotton leaves were obtained was 350 micrometers (i.e., recovery on upper cotton leaves equaled 50 percent). In comparison, the recovery was less than 40 percent for sprays with volume median diameters of 250 micrometers or less. By deductive reasoning, the data in Figure 3 suggest that we are forcing recoveries to be generally 40 percent in an apparent attempt to maintain what is considered to be adequate deposit densities and thus pest control. In reality, this may be justified but we have not found research evidence which will either support or refute the supposition that larger volume median diameters than are typically used can be beneficial.

To our surprise, the deposits on upper cotton leaves (Figure 3) appear to be somewhat larger than corresponding deposits on inert targets for comparable volume median diameters. Due to the small amount of data for deposits on cotton and the fact that we had to estimate some volume median diameters, we do not consider this result to be irrefutable.

The data of Cadogan *et al.* (1986) for aerial deposits of oil and water sprays demonstrate the combined effect of small droplets and high (65 feet) flight heights on deposit recovery. They used a Micronair® unit to create small droplets (deposited volume median diameters ranged from 43 to 147 micrometers) for use in forest insect control. Their deposits across a 460 feet wide sampling area ranged from 1 to 15 percent and averaged 5 percent of the amount applied for 17 tests. Their recovery data seem to be reasonable, based on their droplet sizes and flight height, when compared with the data in Figure 3.

The corresponding literature for quantified spray deposits on cotton or similar plants for ground sprays is also very limited even though we found several papers where deposit-density or percent-area-covered data were used to evaluate spray deposits. Smith *et al.* (1977b) measured on-plant deposits for nozzle-pressure combinations of TX-1 at 80 pounds per square inch, TX-2 at 60 pounds per square inch and TX-4 at 54 pounds per square inch. The corresponding recoveries at the top of soybean plants were 72, 50 and 45 percent for estimated volume median diameters of 70, 87 and 110 micrometers, respectively. They used more than one nozzle over each row which may have altered the recoveries as compared with the usual one nozzle per row applications. As expected, these recoveries are considerably larger than corresponding aerial recoveries for similar volume median diameter sprays (Figure 3) because the spray was released about 15 inches above the plant canopy. Johnstone (1977) sampled leaves from entire cotton plants and reported leaf recoveries of 89, 67 and 74 percent of the amount applied for rotary atomizer sprays with volume median diameters of 90, 86 and 60 micrometers, respectively. Because the spray was released over six alternate middles, a given target may have received some spray from several or all of the passes. Thus, these data are representative of "field" deposits but does not address the lateral displacement of 60-90 micrometer droplets. Ware *et al.* (1975) also studied whole plant recoveries on cotton using TX-6 nozzles at 40 pounds per square inch on a ground, boom sprayer. They reported that 39 percent of the spray was deposited on plants and 34 percent on the soil for short (29 inches) plants for a total of 73 percent

of the amount applied. For mature plants (49 inches tall), the recoveries were 83 percent on plants and 6 percent on the soil for a total of 89 percent. They concluded that their recovery rates for ground, boom sprayers were much larger than for aerial applications.

Most of the recovery data have been reported as means and the variation about the mean is not generally indicated. One may wonder how uniformly the spray needs to be applied in order to attain the best insect or mite control. Some work is in process to address this question but no prior data have been found in the literature. Some data on the variation in deposits on plant canopies are available. The raw data from the studies conducted by Smith *et al.* (1977b) were used to calculate the coefficients of variation (i.e., standard deviation of deposits on soybean leaves multiplied by 100 divided by the mean deposit) for the first replication of treatments 1 to 3 (cone nozzles) at the top, middle and bottom. At the top, middle and bottom (i.e., about 3 feet tall plants with bottom samples taken at one foot), the range of the coefficient of variation values for the three ground, boom sprays were 29 to 53, 50 to 95, and 104 to 117 percent, respectively. These data indicate that the spray deposits on leaves are considerably more variable at the middle and bottom locations than at the top. The increased variation for the lower positions on the plant is to be expected due to the variable screening effect of the leaves located above a given sampling location on a plant. Uk and Courshee (1982) reported that coefficient of variation values (for one aerial treatment along three sampling lines) ranged from 35 to 46 percent for deposits on upper cotton leaves. Cadogan *et al.* (1986) took samples from horizontal targets and reported both deposit means and standard deviations. The coefficients of variation for their data were found to range from 44 to 155 percent and averaged 93 percent for the small droplets and high flight heights they used. Yates (1962) reported coefficient of variation values for three aerial sprays (artificial targets on the ground) which ranged between 15 and 45 percent for swath widths of 40 feet. Smith (1983) reported that the coefficient of variation values are linearly related to the difference between the maximum and minimum deposits in a given data set. This means that a coefficient of variation of 30 percent indicates that the maximum deposit is about 2.7 times larger than the minimum deposit (Smith, 1983, 1992). If a 1.5x dosage represents effective insect or mite control, then larger deposits indicate wasted chemical and smaller deposits represent reduced pest control. Thus, our objectives should continue to focus on applying chemicals as uniformly as possible until we know whether or not less uniformly applied sprays are equally effective. A desirable level of uniformity is represented by a coefficient of variation no larger than 15 percent.

Because insects and mites are often not located on the upper part of the plants, one needs to know what magnitude of deposits are needed for the lower plant canopy locations. The penetration of sprays into plant canopies may be studied effectively by referencing all deposits to the amount deposited on the top of a canopy (Figure 4). The data shown in Figure 4 are from a variety of sources and include aerial, ground, water, and oil applications for a variety of canopy types including hardwoods, cotton, and soybeans. We did not include deposits from plants such as corn, milo, and tomatoes,

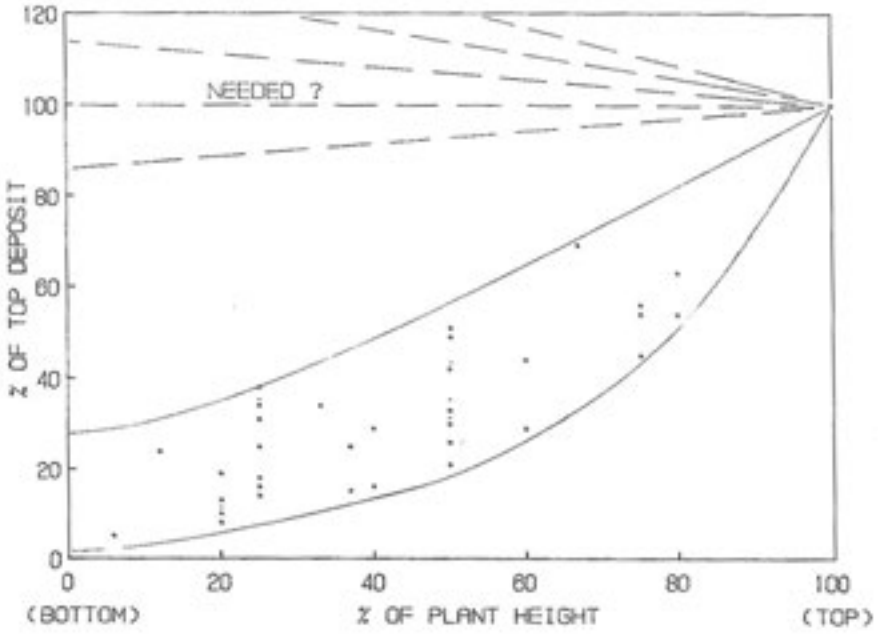

Figure 4. Penetration of sprays into cotton or cotton-like canopies for aerial and ground sprays based on results presented by Bouse (1969), Burt and Smith (1974), Smith *et al.* (1977b), Uk and Courshee (1982) and Ware *et al.* (1984).

because they are not structurally similar to cotton. The data in Figure 4 indicate that the penetration of several different types of spray applications are similar. For example, deposits half way up the plant for mature, overlapped canopies, ranged from 20 to 50 percent of the amount deposited on top of the plants and averaged about 35 percent. At the soil surface, or bottom of the plant, the deposits would be expected to be not greater than 25 percent of the top deposit and perhaps as small as 3 to 5 percent. The canopy penetration data illustrates why it is difficult to control older larvae which are located on the lower plant parts.

The upper part of Figure 4 indicates hypothetical deposit distributions which might be desirable, especially for larger larvae which have moved down to the middle or lower canopy locations. We have not found any data that indicates the most desirable vertical distribution of chemical for any plant type-pest combination. Even if the most desirable vertical distribution were known, the required application equipment and techniques may not be economically feasible. Thus, for the forseeable future, applicators are likely to be constrained to spray distributions within cotton canopies similar to those shown in the lower part of Figure 4. It seems apparent that fourth to fifth instar bollworm/tobacco budworm larvae will not be killed below some height in the plant

canopy due to the severely reduced spray deposits at the lower levels and the fact that most of the larvae at the lower levels are located in bolls.

APPLICATION SAFETY

The safety aspects associated with the application of chemicals can be divided into two broad categories. These two groups involve situations where: (a) common sense and forethought are the primary considerations and (b) guidelines are not obvious and the applicator must rely on research data for assistance.

Handling, Flagging and Container Disposal — The first category involves the safety aspects where there is potential for exposure by direct contact during handling and application — manual transportation of pesticide containers, mixing and loading, flagging fields for aerial sprays and disposing of "empty" pesticide containers. With these types of operations, an individual will not normally encounter a serious safety problem if he: (a) exercises good judgement; (b) uses common sense; (c) thinks before he acts; (d) reads the pesticide container's label; and (e) is well informed about the relative toxicity of the various pesticides being applied. For example, good judgement indicates that one should not handle a pesticide container, especially one containing a highly toxic pesticide, without wearing adequate protective clothing. Unfortunately, this is not always done! Some research groups who have studied worker safety problems associated with the application of pesticides include Wolfe *et al.* (1967), Brazelton *et al.* (1981), and Lavy *et al.* (1982). In general the mixing and loading operation is more dangerous than operations associated with mechanical repairs/adjustments, piloting or operating a sprayer, flagging or working in the field after the reentry period as specified on the pesticide label. Because the mixing and loading operations normally cause the highest level of worker exposure, a wide variety of closed mixing systems have been developed in an attempt to reduce worker exposure levels. Those systems which open, empty and rinse the pesticide container while it is inside the closed system are more likely to reduce exposure levels than systems which require a person to insert a probe into the container. Brazelton *et al.* (1981) concluded that training workers on the proper use and maintenance of closed systems was essential for further reducing the exposure to mixers and loaders.

Spray Drift, Field Reentry and Worker Exposure — The second safety area relates to concerns such as drift, operator exposure, and the establishment of worker reentry periods. For these types of problems, the applicator typically needs some research information before a good decision can be reached. For example, it is not obvious whether the wind velocity, spray release height, atmospheric stability, relative humidity, temperature, or droplet size distribution is the most important variable for decreasing spray drift deposits (Smith *et al.*, 1993).

Spray drift has been, and is presently, of formost concern when herbicides are being applied. Herbicide damage to crops is visible and may be traceable to a given spray application. On the other hand, there has been less concern over drift when insecticides, miticides or fungicides are applied. The fact is, however, that the droplet size

distribution used for applying these latter types of chemicals typically contains many more drift-prone, small droplets than are found in herbicide sprays applied with similar equipment (i.e., air or ground).

The increased concern about ground water contamination, human exposure and regulation of the "inert" ingredients in pesticide formulations has caused concern among regulatory agencies and the general public about spray drift from all pesticide applications.

The subject of spray drift has received much attention over the past 40 years. The current knowledge about the variables influencing spray drift from aerial applications has been summarized by Ware *et al.* (1983). Even though some of the more important variables are known, the relative importance of the relevant, independent variables was not known until recently (Smith *et al.*, 1993). Several computer simulation models have been developed to assist with aerial spray drift decisions (Teske, 1984; Akesson and Gibbs, 1988; Saputro *et al.*, 1991). However, most of the aerial drift studies have consisted of a few combinations of the independent variables and, as such, do not allow for the development of a comprehensive set of data. Such a statement is not intended to be a reflection on any of the researchers involved; rather it is a statement of where we are and what is needed. Additional comprehensive research in this area is warranted and needed.

Spray drift deposits associated with ground sprayers has received more research emphasis than aerial drift even though drift from aerial sprays typically is several times greater than that from functionally similar ground applications. On the other hand, ground applications using mist blowers may cause more drift than the corresponding aerial sprays.

Several large, ground sprayer studies have attempted to delineate the relative importance of several variables on spray drift (Threadgill and Smith, 1975; Bode *et al.*, 1976; Smith *et al.*, 1982a). Threadgill and Smith (1975) applied ultra low volume sprays over a cotton canopy in 74 tests with droplet sizes ranging from 27 to 200 micrometers. They reported that: (a) drift deposits were highest for stable atmospheric conditions; (b) increasing the mean droplet size decreased drift deposits; (c) increasing wind speed decreased drift deposits; and (d) drift deposits decreased as the vertical component of the wind speed decreased. Bode *et al.* (1976) studied drift deposits from hydraulic nozzles in 30 tests. Of the 15 variables and combinations of variables which they evaluated, the most important (i.e., highest ranked) variable was boom height. The interaction of boom height and wind speed was second; application volume was third; and wind speed was the fourth most important variable. They did not evaluate the effect of droplet size *per se* even though they varied atomization pressures and nozzle types and used a thickener in some tests. Smith *et al.* (1982a) ran 99 tests using hydraulic atomizers and evaluated 18 independent variables. They reported that the three most important drift related variables (in decreasing order of importance) were boom height, horizontal wind speed and vertical nozzle orientation. They did not find relative humidity, droplet size, volume applied, or atmospheric stability to be significantly related to the magnitude of spray drift deposits.

A word of caution is in order at this point. Some individuals have assumed that results from drift studies with ground equipment are directly applicable to aerial appli-

cations. Such extrapolations are discouraged. Aerial sprays are released much higher than ground boom sprays allowing more time for evaporation and cross winds to affect the spray droplets. Also, the air turbulence created by aircraft is much greater than the tubulence associated with ground sprayers. For example, atmospheric stability is frequently reported to be an important drift variable for aerial applications but it is seldom reported as such for ground boom sprays.

The exposure of operators and other workers to pesticides in either the concentrate or dilute form is another important safety area. Wolfe *et al.* (1967) reported that dermal exposure was much greater than respiratory exposure. However, they cautioned that equivalent doses are absorbed more readily and more completely through the respiratory tract than through the skin. In reviewing the relevant literature, no data related to the effect of sprayer speed, wind speed, wind direction and atmospheric stability on the dermal or respiratory exposure of a ground or aerial sprayer operator were found. Some data are available on exposure levels for various types of sprayers but, one would think that other test conditions may be more important than the type of sprayer used.

Most of the current guidelines for drift, exposure and reentry concerns involve subjective decisions. For example, ideally it would be desirable to have no drift, but in practice attempts are made to minimize it to an 'acceptable' level. The subjective decision process must continue until sufficient information is available to mathematically describe the crop, lake, river, and human exposure levels involved under a given set of application conditions. The time frame for the availability of such information will depend upon the support for such work. Drift and exposure studies are both expensive and time consuming.

CHEMIGATION

Chemigation may be defined as the application of crop production/protection chemical through an irrigation system. The types of chemigation referred to include fertigation (fertilizers), herbigation (herbicides), fungigation (fungicides), insectigation (insecticides), and nemagation (nematicides). The basic idea of applying a chemical through an irrigation system is over thirty five years old (Bryan and Thomas, 1958). Surface and trickle/drip type irrigation systems can be used for fertigation and herbigation in those cases where the chemical is needed on or within the soil. However, an overhead type of irrigation system can be used for any chemigation application if the pesticide will not cause damage to the crop and the formulation is appropriate.

The amount of water applied during each chemigation application varies from about 0.1 inches (2,715 gallons per acre) to 0.75 inches (20,634 gallons per acre). The chemical being applied must be metered accurately so that the correct amount is applied per unit area of land or crop. Many pumping systems are available to meter the chemicals.

A considerable amount of research has been conducted on the chemical formulations which are most suitable for chemigation applications. For soil applied chemicals, the type of formulation does not appear to be overly important. However, for foliar applied chemicals, the most consistently positive results have been obtained when the

technical chemical was formulated in an oil without the addition of any emulsifier (Threadgill, 1985). Some work has been done on the method in which the chemical is injected (i.e., nozzle size or orientation and injection pressure) but these effects are not likely to be as important as formulation effects.

Safety is an important consideration when contemplating the use of chemigation systems. These safety considerations are discussed in the American Society of Agricultural Engineer's (ASAE) publication, Engineering Practice EP409 (ASAE, 1983). The primary safety considerations include a backflow prevention system and an interlocking injection system. The backflow system is designed to prevent any chemical from returning to the water supply when the water pump is not in operation. The interlocking injection system stops the chemical pump any time the water pump is inoperative so that chemical is not wasted. The Environmental Protection Agency's safety requirements for chemigation are the same as the requirements imposed by each state.

Several types of irrigation systems are capable of delivering relatively uniform amounts of chemical-water mixtures to a soil surface. The degree of uniformity has been favorably compared to that obtained with ground sprayers and is generally more uniform than that from typical aerial sprays (Threadgill, 1985). However, irrigation systems such as traveling guns, which depend on long spray trajectories usually will not provide a high degree of uniformity of the spray deposits (Shull and Dylla, 1976; Smith, 1989). Also, there is a void of information regarding chemical deposits on cotton plants resulting from chemigation applications. Additional research is warranted to assure that adequate on-target deposits are being attained and that ground level chemical deposits are reasonable.

Center pivot irrigation systems have been used extensively to study pest control resulting from chemigation applications on about 20 crops (Johnson *et al.*, 1986). Such application systems have been shown to be more economical than ground or aerial applications when: (a) more than one chemical application is needed per season and (b) the crop needs irrigation water. Other reported advantages for chemigation include reduced soil compaction and plant damage (as compared with ground sprayers), elimination of the need to incorporate some herbicides and reduced pesticide exposure. The most important disadvantages include: (a) greater management skills are required; (b) additional equipment must be purchased; (c) the possibility of contamination of the water supply if the safety equipment is not adequate and operating properly; (d) possible increased application time; and, (e) possible unnecessary water applications.

Chemigation is another proven chemical application system and can offer net advantages for some farmers.

RELEASE OF PARASITES AND PREDATORS

Some of the most promising alternative methods of cotton insect control involve the mass release of insects. Two of the most widely studied ones in the cotton production system are: (a) augmentative releases of entomophagous insects (insects that feed on

other insects; Stinner, 1977); and (b) incorporation of sterile or sterile progeny-producing insects (Knipling, 1979) into natural populations. Although the biological and ecological factors influencing the efficacious use of these different control methods may be method-dependent, the application problems associated with mass releases of insects are similar. However, they are drastically different from those associated with the application of chemical insecticides. The distribution of competitive and healthy insects over target areas (often encompassing large acreages) will require application methods carefully developed to prevent damage to the insects, yet allow for efficient delivery of large numbers of insects to target areas in a rather short period of time. This requires a thorough knowledge of the release insect's biology and movement, as well as creative procedures and equipment specifically designed for the particular release insect-pest insect situation. Unfortunately, the efficacy of these control methods cannot usually be determined until efficient application methods are developed. Often, the required knowledge concerning insect biology and the effect of various environmental and physical stresses on the release insect's survival and competitiveness are unknown.

Most methods of insect control that include mass releases of insects require tremendous investments in research and development. Probably the two most researched examples in the cotton production system are augmentative releases of *Trichogramma* spp. for control of bollworm and tobacco budworm (Ridgway *et al.*, 1977) and mass releases of sterilized boll weevils in areawide suppression programs (Griffin, 1984; Villavaso *et al.*, 1986). Other notable examples in the cotton production system where release technology has received research attention are mass releases of *Chrysoperla* (=*Chrysopa*) spp. (lacewing predators; Ridgway and Jones, 1969; Kinzer, 1976) and *Trichogramma pretiosum* (egg parasites; Bouse and Morrison, 1985) for bollworm/tobacco budworm control and mass releases of sterile pink bollworms *Pectinophora gossypiella* Saunders (Ables *et al.*, 1979).

In a review of the methods used to release entomophagous insects, Ables *et al.* (1979) described three critical phases of the application process. First, the insects must be mass-produced in sufficient numbers and quality to allow field releases. Second, the quality of the insects must be preserved during transportation from the insectary to the release site. And third, the insects must be evenly and efficiently distributed over the target area. All three phases require technology and equipment specifically designed for the particular release-insect/pest-insect situation.

Most of the published scientific literature on mass releases of insects involve experiments where insects were released by various manual methods. For example, Stinner *et al.* (1974) manually released *Trichogramma pretiosum* Riley parasitized *Sitotroga* eggs for control of bollworm/tobacco budworm on cotton. Using insulated containers, they transported the parasitized eggs to cotton fields and emptied the containers onto plants. Villavaso *et al.* (1986) released sterilized boll weevils by attaching paper bags containing the weevils to cotton plants. Similar methods have long been used for various manual releases of entomophoagous insects.

Although release technology has evolved to the point that mechanical methods of release have been utilized for various programs, the technology associated with large

scale releases of *Trichogramma* spp. is probably the most refined. These mechanical releases have involved both ground (Ables *et al.*, 1979; Jones *et al.*, 1977) and aerial (Ables *et al.*, 1979; Bouse *et al.*, 1981; Jones *et al.*, 1979; and Luttrell *et al.*, 1980) application methods. Since the specific procedures are described in several other references (Ables *et al.*, 1979; Bouse and Morrison, 1985; Bouse *et al.*, 1981; Jones *et al.*, 1979; Ridgway *et al.*, 1977; Bouse *et al.*, 1980 and King and Coleman, 1989), they will not be repeated here. It is important to emphasize the need to protect the release insect. This required considerable research in the development of effective production and transportation methods (Morrison *et al.*, 1978).

Ground releases have been made by automatically dropping containers from moving vehicles, by spraying liquid suspensions and broadcasting various granular mixes. The advantages and disadvantages of these techniques were discussed by Ables *et al.* (1979). Aerial releases have usually involved the dispensing of containers, the dispersal of granular mixes or the free release of entomophagous insects. Again, these methods are discussed by Ables *et al.* (1979). When granular mixes are used, the insects are usually mixed with some inert dispersal medium (e.g. wheat bran flakes). This sometimes requires that the insect be attached to the the inert carrier. Free releases usually involve the use of a venturi spreader similar to those used for application of insecticide dusts or granules.

The development of application methods for mass release of entomophagous insects is complicated because the equipment and methods may need to be specifically designed for each release-insect/pest-insect situation. As a result, the application technology associated with mass release of entomophagous insects is rather limited. The most elaborate application systems are those associated with mass releases of *Trichogramma* spp. (Bouse and Morrison, 1985).

SUMMARY

Most of the pesticide application research has been conducted during the last forty years. Those papers/reports related to application equipment, spray atomization and on-target deposition represent only one or two percent of all of the scientific publications related to insect/mite control on cotton. There are thousands of possible insect-crop-insecticide-formulation- application system combinations. Only a relative few of these combinations have been evaluated in a comprehensive manner. It is hoped that a recent increase in USDA-ARS funding for application research will have a positive impact on some of these problems.

Residual contact accounts for about 80 percent of the bollworm/tobacco budworm and boll weevil control with chemical insecticides. The remaining 20 percent is attributable to direct impingement on the insect's body. Such data have helped define the intended target for the crop-insect-insecticide combinations studied. Most of the questions regarding the optimal deposition of spray deposits on or within plant canopies currently remain unanswered. Much research remains to be completed toward the development of complete, quantified data sets from which the effects of application,

formulation and meteorological variables on spray deposits — and, in turn, the effect of such deposits on insect/mite control— can be determined.

There are about 22 categories, 225 products or product lines and 1100 scientific papers that relate to adjuvants (materials used with insecticides and miticides to improve their performance). Much of the prior work with adjuvants has been associated with the use of entomopathogens. The use of adjuvants in conjunction with entomopathogens has increased insect mortality in some studies while having no significant effect or a detrimental effect in other studies. Additional research is needed to delineate the effect of adjuvants on: (a) insect/mite mortality per se and (b) on the atomization-deposition-insect behavior process and the effect of these variables on insect/mite mortality.

One microbial insecticide (*Bacillus thuringiensis* Berliner) is commercially available and is used on a limited basis for cotton insect control. Much of the prior laboratory insect mortality-dosage data for microbial insecticides indicates that they are very effective. However, results from many field studies indicate that the level of insect control obtained is less than that which is often needed. The level of insect control obtained on cotton is usually lower than that obtained on soybeans and some horticultural crops. A considerable effort has been devoted to the use of feeding adjuvants, baits, and ultraviolet light protectants, in conjunction with microbial insecticides. Even so, there still appears to be a substantial need to increase the half-life of such insecticides for effective utilization in the field.

Many manuals are available on: the selection, use and care of spray equipment; calibration of sprayers; and spray drift. A list of atomizers and operating conditions which are likely to provide adequate insect/mite control is included in this chapter. Unfortunately, all of the recommendations for aerial sprays are based on atomization or deposition information without regard to the level of insect or mite control obtained.

Dust formulations are not used widely today due to their relatively poor deposition efficiency (i.e., generally less than 25 percent of the amount applied). Spray droplets greater than about 100 micrometers are needed for use with ground boom sprayers in order to minimize spray drift. The corresponding desired lower limit for aerial sprays is about 150 micrometers. The latter lower limit suggests that aerial sprays with volume median diameter equal to or greater than 300 micrometers are needed to minimize spray drift. Electrostatic charging of sprays has shown promise in some studies but additional research (i.e., engineering and entomological) is required before this technology is usable at the farm level.

The on-plant deposition efficiency for typical aerial and ground sprays are on the order of 40 and 85 percent, respectively. Future research in this area needs to focus on: (a) the upper limit for spray droplet size with respect to spray drift; (b) on-target deposition; and (c) insect/mite control. This type of research is needed because most researchers in the pesticide application - pest control area believe that the public's concern over environmental, safety and ecological issues will continue increase during the next ten or more years.

A clearer understanding about the effects of the physical properties of the spray liquid on the resulting droplet size distribution is needed. Results from several atomiza-

tion studies indicate that the effect of a given physical property of a spray may be confounded with atomizer types. Progress in obtaining a comprehensive understanding of the spray atomization process for a variety of liquids would provide part of the foundation needed to improve future insecticide applications on cotton and other crops.

At the present time, it is essentially impossible to obtain uniform spray deposits under field conditions. Coefficients of variation for aerial and ground sprays often exceed 30 percent. A coefficient of variation of 30 percent indicates that the maximum deposit sampled is about 2.7 times larger than the minimum deposit. Such extremes in the deposits suggest that pesticides are not being used effectively either due to over- or under- dosage effects. Some limited simulation work has been done to estimate the effect of deposit nonuniformity on insect control. However, results from field evaluations of similar deposit variation work are not currently available.

Some of the safety aspects associated with the application of pesticides can be overcome by the use of good, common sense. However, sound research data is needed to provide safety guidelines for problems such as reentry intervals, contamination, drift and human or animal exposure. The operator exposure literature is woefully incomplete due to: (a) the limited number of studies which have been run; and (b) the omission of either the measurement- or reporting- of key variables which affect the magnitudes of deposits on sprayer operators. Closed-systems used for mixing and loading pesticides can substantially reduce exposure levels of workers associated with these operations. There remains a continuing need for a comprehensive, aerial spray drift data set in order for researchers and extension personnel to be able to provide more substantial advice for aerial applicators and the producers whom they serve.

Chemigation has been shown to be an effective method for applying certain formulations of insecticides and miticides. Such applications can be economical, especially if the crop also needs to be irrigated. The use of proper safety equipment on chemigation rigs is essential (or manditory in most cases) so that the water supply source is not inadvertently contaminated.

Aerial and ground methods have been developed for the release of some parasites and predators. Other equipment may be needed in the future. For future equipment development research, the primary design emphasis should be focused on protection of the released predator or parasite.

Chapter 11

PHEROMONES AND OTHER BEHAVIOR-MODIFYING CHEMICALS IN COTTON PEST MANAGEMENT

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INTRODUCTION

The importance of behavior-modifying chemicals in cotton insect management lies in their potential to contribute to more effective control measures while reducing reliance upon insecticides. These materials can increase the efficiency of insecticide applications and can provide alternative means of suppression that may be more effective, more economical, and more environmentally and socially acceptable than the use of insecticides alone. Practical uses of behavior-modifying chemicals generally involve surveillance or suppression tactics. Surveillance tactics usually involve trapping and can be used for detection, monitoring and prediction. Suppression tactics may act: (a) directly on the pest population (e.g., mass trapping, mating disruption and feeding or oviposition deterrents); (b) indirectly by augmenting or manipulating the behavior of natural enemies; or (c) in conjunction with conventional pesticides as attracticides or bioirritants. To be successful, practical application of behavior-modifying chemicals requires consideration of a wide range of factors. These factors include the behavior, dispersal, distribution, host range and density of the pest insect; the nature of the pest complex; the identity, composition and formulation of the chemicals; the timing of applications; and the environmental, economic and social consequences of their use. Pheromones and other behavior-modifying chemicals are being used in a variety of cotton insect management programs.

Semiochemicals are a group of behavior-modifying chemicals defined as naturally occurring substances that mediate interactions between organisms (Law and Regnier, 1971). Unlike hormones or neurotransmitters, which are produced by and act within an organism, these chemicals are emitted by one organism and effect interactions with other organisms of the same or different species. Chemicals effecting intraspecific interactions are referred to as pheromones (Karlson and Butenandt, 1959; Nordlund

and Lewis, 1976), while those that mediate interspecific interactions have been termed allelochemics (Whittaker and Feeny, 1971) or, more recently, allelochemicals. Allelochemicals, in turn, are classified on the basis of whether the response evoked favors the emitter or the receiver of the chemical. A kairomone elicits a response favorable to the receiver (Brown *et al.*, 1970); the response to an allomone benefits the emitter (Brown, 1968); and the response to a synomone is favorable to both organisms (Nordlund and Lewis, 1976). These terms are not mutually exclusive. For example, a substance emitted by a female insect that is used by the male in finding a mate is a pheromone. If the same substance is also involved in the mechanism whereby a parasite or predator of that insect locates its prey, it is a kairomone. A synthetic copy of a semiochemical is referred to by the same name as the natural material; e.g., a synthetic pheromone is the synthesized version of the natural compound emitted by the insect. However, some synthetic compounds that affect insect behavior are not known to occur naturally in the organisms involved and therefore are not semiochemicals. Among these are the parapheromones, which are compounds that mimic pheromones in their activity but have not been shown to be emitted by the insect. Synthetic attractants and synthetic repellents are other examples of behavior-modifying chemicals that are not classed as semiochemicals. The practical application of pheromones on a wide range of crops has been reviewed in some detail elsewhere (Ridgway *et al.*, 1990a). The behavior-modifying chemicals most frequently associated with cotton insects in the United States are pheromones and kairomones, and the chief focus of this chapter will be on these semiochemicals.

DELIVERY SYSTEMS

To use behavior-modifying chemicals effectively in the management of cotton pests, careful thought must be given to the development of appropriate delivery systems. A controlled-release formulation is usually necessary, because most of these chemicals are used at very low dose rates, are volatile and are subject to environmental degradation. For active materials made up of several components, the ratio at which these components are emitted may need to be kept constant despite differences in their volatility. The type of formulation and its method of use will affect the design parameters of the delivery system, as will the behavior patterns of the insect. For example, many of the factors that must be considered in developing an attractant for a trap may be different from those involved in formulating a dispenser for use in preventing mating through communication disruption.

The delivery system should be compatible with regular agricultural practices. For baits in traps or for dispensers that must be hand-placed, ease of handling is a major factor. For material to be broadcast, it is desirable to have a sprayable formulation, with dispensers of appropriate particle size, together with compatible stickers and other adjuvants. For some types of delivery systems, a sprayable formulation has not been practical. It has been necessary to develop special dispersal systems for some larger non-sprayable solid particles and fibers.

Most controlled-release systems may be classified as belonging to one of four basic types (Zeoli *et al*., 1982; Leonhardt, 1990): (a) reservoir systems without a rate-controlling membrane, e.g., hollow, open-ended fibers or capillaries; (b) reservoir systems surrounded by a rate-controlling membrane, such as capsules; (c) monolithic systems in which the active chemical is dispersed throughout an inert matrix; and (d) laminates, in which an inner reservoir containing the active material is sandwiched between two outer polymeric layers. In the first type, the active material evaporates from the liquid surface within the tube and diffuses to the end of the tube, where it is released; the rate of release is determined by the rate of evaporation and the rate of diffusion to the end of the tube. In reservoir systems with a rate-controlling membrane, all or part of the wall of the reservoir is made of a permeable polymer through which the active material diffuses. The release rate is determined to a great extent by the nature of the polymer and the thickness and surface area of the wall. A variety of these systems are in use, including sealed polyethylene tubes, bags, or vials and polymer-coated microcapsules of various types. In the third type of system, the active material is dispersed in an inert matrix; emission rates are dependent on the rate of diffusion within the matrix to the surface. A common example is a rubber cap or septum impregnated with pheromone, but these require precautions against degradation of pheromone components by substances used in the manufacture of the rubber. In the laminate dispensers, the rate of emission is controlled by the dimensions of the outer polymer layers, the nature of the polymer and the concentration of the active ingredient in the reservoir layer. With variations in particle size and in dispenser shape, systems representing these four types have been used in a wide range of applications. Suitability of a system for a given application must be determined in the field.

In order to obtain meaningful data when using different delivery systems and to assure activity for the desired length of time, performance criteria for the controlled-release dispensers must be specified (Leonhardt *et al*., 1990). Important factors are the concentration and purity of the active material, the rate of emission, the ratio in which the components of a mixture are emitted, and the duration of effectiveness of the dispenser. Performance standards developed in laboratory and field studies give assurance of the reliability of a delivery system. A number of specific controlled studies are available that illustrate approaches to developing controlled-release dispensers for behavior-modifying chemicals (Coppedge *et al*., 1973; Hendricks *et al*., 1989; Leonhardt *et al*., 1985, 1987, 1988, 1989).

ARTHROPOD PESTS

The major research emphasis on behavior-modifying chemicals of arthropod pests of cotton in the United States has been on the sex and aggregating pheromones of the boll weevil, *Anthonomus grandis grandis* Boheman, and the sex pheromones of three lepidopterous insects, the pink bollworm, *Pectinophora gossypiella* (Saunders), the bollworm, *Helicoverpa* (=*Heliothis*) *zea* (Boddie), and the tobacco budworm, *Heliothis virescens* (F.). Significant, but more limited, efforts have been directed

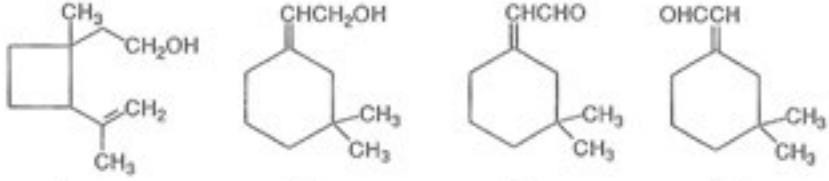
towards pheromones of *Lygus* bugs, stink bugs and mites and towards kairomones for parasites and predators. More recently, some potentially important research on allelochemicals that may be very useful as attractants and feeding stimulants for the boll weevil and the bollworm is receiving increased attention.

BOLL WEEVIL

The boll weevil is a serious pest of cotton that occurs in most cotton growing states in the United States. However, areawide management or eradication programs have essentially eliminated the boll weevil from the Carolinas, most of Georgia, north Florida, southeastern Alabama, California and Arizona. Adults, which overwinter in crop remnants or other debris near cotton fields, emerge in the spring and feed on cotton plants, doing their greatest economic damage when the squares and bolls appear. Females oviposit (lay eggs) into the squares or bolls, where the larvae hatch, feed and then pupate. Adults emerge, feed and oviposit to continue the cycle. In some areas there may be seven or more generations per year.

Observations made in a simple but elegant experiment conducted in 1963 (Cross and Mitchell, 1966) suggested the presence of a male-produced, wind-borne boll weevil pheromone. In subsequent laboratory studies (Keller *et al.*, 1964), an active airborne substance emitted by males was obtained by drawing air over caged males and through a column of activated charcoal for three weeks. Extraction of the charcoal and evaporation of the solvent yielded a residue that stimulated and attracted female weevils.

The boll weevil sex pheromone was later identified (Tumlinson *et al.*, 1969) as a mixture of four components (Figure 1). In laboratory tests, the optimum ratio of these components was found to be 9:7:12:12 (Tumlinson *et al.*, 1969). However, it was shown that the omission of the third compound had no significant effect on attractancy in the field (Dickens and Prestwich, 1989), and that the ratios could be varied considerably without significantly affecting attractancy in the field (Hardee *et al.*, 1974). Depending on the time of year, this boll weevil pheromone functions both as a sex pheromone and as an aggregating pheromone. In the spring and fall, traps baited with males attract both sexes of overwintered adults. In mid-season (during the fruiting season), mostly females are attracted (Mitchell and Hardee, 1974; Hardee, 1975).



I II III IV

Figure 1. Chemical structures of the four grandlure components: (I), *cis*-2-isopropenyl-1-methylcyclobutaneethanol; (II), *(Z)*-3,3-dimethyl-$\Delta^{1,5}$-cyclohexaneethanol; (III), *(Z)*-3,3-dimethyl-$\Delta^{1,5}$-cyclohexaneacetaldehyde; and (IV), *(E)*-3,3-dimethyl-$\Delta^{1,5}$-cyclohexaneacetaldehyde.

Furthermore, the attractancy of the pheromone is increased in the presence of host plants or plant chemicals (Coppedge and Ridgway, 1973; Dickens, 1989).

The synthetic pheromone, grandlure, has been used, or can potentially be used, in a variety of ways to assist in boll weevil management. It is used in traps to detect the presence of boll weevils (Dickerson *et al.*, 1987a) and, in areas where the pest is already established, to monitor population densities (Ridgway *et al.*, 1985). Traps have also been used in attempts to suppress populations through mass trapping of adults, although this technique shows promise only at low population densities (Leggett *et al.*, 1988). Other potential population suppression techniques using grandlure include mating disruption (Huddleston *et al.*, 1977); trap cropping, i.e., use of the pheromone to attract weevils to a small portion of the crop where they can be destroyed (Gilliland *et al.*, 1974); and attracticides, which combine the pheromone and/or host-plant chemicals with an insecticide (McKibben *et al.*, 1985; Lusby *et al.*, 1987; Ridgway *et al.*, 1990b). Large scale field trials are under way in Mississippi to evaluate the use of grandlure with a toxicant applied to a wooden surface (bait stick) and distributed in the field as point sources (Personal communication, James W. Smith, USDA, ARS, Boll Weevil Research Unit, Mississippi State, Mississippi).

Grandlure is currently in widespread use in traps for both monitoring and mass trapping. Although a range of commercial dispensers is available, an improved plastic laminate dispenser and a polyvinyl chloride dispenser (Dickerson *et al.*, 1987b; Leonhardt *et al.*, 1988), each containing 10 milligrams of grandlure, are used predominately. Monitoring with pheromone traps as a guide to application of insecticides for overwintered boll weevil control is in use in a number of states (Ridgway *et al.*, 1985). Pheromone traps also are utilized for detection, monitoring and/or mass trapping in a number of areawide boll weevil population suppression programs, including ones in the Southeast, Southwest, and Texas. The general use of grandlure in traps for detection, monitoring and mass trapping has been reviewed elsewhere (Ridgway *et al.*, 1990b).

Operationally, the most extensive use of boll weevil pheromone traps has been in the Southeastern Boll Weevil Eradication Program which began in 1978. The program has essentially proceeded in three phases: (a) eradication trial in North Carolina and Virginia; (b) expanded program into southern North Carolina and South Carolina; and (c) expanded program into Georgia, Alabama and Florida (Figure 2).

The boll weevil eradication trial was conducted in North Carolina and Virginia in 1978-1980. The technology applied included pheromone traps for surveillance and suppression, release of sterile insects and insecticide treatments of overwintering adults on a mandatory basis (USDA, 1981a). The cotton acreage involved in the trial area (See Figure 2) was about 12,000 acres (4,800 hectares) in 1978; after the initial trial was completed, the program was continued and the area covered was expanded. The acreage planted to cotton in the area covered by the initial trial had increased to 70,000 acres (28,000 hectares) by 1987 (Planer, 1988). The trial was generally considered to be an economic (Carlson and Suguiyama, 1985) and biological (USDA, 1981b) success, although there was some disagreement about the interpretation of biological results (National Research Council, 1981; USDA, 1981b).

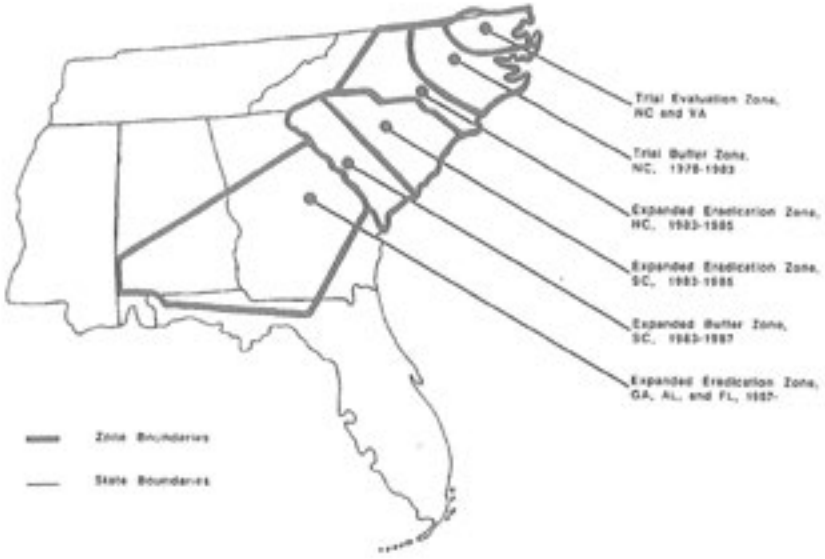


Figure 2. Diagram of the state boundaries (light line) and zone boundaries (heavy line) within the Southeastern Boll Weevil Eradication Program. (From Ridgway *et al.*, 1990b.)

In the eradication trial, traps were initially deployed at the rate of one per 8 to 10 acres (3 to 4 hectares) around fields to aid in scheduling fall diapause boll weevil applications. In the spring of 1979 and 1980, one trap per acre was placed around fields to monitor populations. After cotton was growing two traps per acre were placed in the fields to maximize detection and for possible suppression through mass trapping. In the fall, traps were again placed around fields at one trap per acre. When reproduction of the boll weevil had been eliminated in an area, the trap density was reduced to one trap per 5 to 10 acres (2 to 4 hectares), and the traps were used primarily to detect possible reintroductions. The extremely low numbers of boll weevils that were detected in the original trial evaluation area in North Carolina reflected the efficacy of the program in eliminating reproducing boll weevil populations (Table 1). The increased trap captures in the buffer area in 1982 and 1983 and overall increases in boll weevil populations outside the program area in southeastern North Carolina during those years probably reflect the reduced boll weevil suppression efforts in the buffer area. The value of the pheromone traps in detecting reintroduced boll weevils so that measures can be taken to prevent reestablishment of boll weevil populations has been demonstrated repeatedly in the trial evaluation area. Specific cases for 1984 and 1985 are discussed by Dickerson *et al.* (1986). Results of reductions in boll weevils in the expanded eradication zones in North Carolina and South Carolina indicated that the program also was effective in those areas (Dickerson *et al.*, 1986, 1987a). Further, an

Table 1. Boll weevil capture in fields in the Southeastern Boll Weevil Eradication Trial Evaluation Zone, 1979-1989. (From Ridgway *et al.*, 1985; Dickerson *et al.*, 1987a; W. A. Dickerson, personal communication[1].)

Year	Acres	No. of fields trapped	Percent of fields at three weevil capture levels (no. of weevils per field)		
			0	1-5	>5
1979	15,200	1,020	99.12	0.88	0.00
1980	26,700	1,775	99.98	0.06	0.06
1981	35,700	2,600	99.00	0.96	0.04
1982	37,800	3,000	91.47	6.66	1.87
1983	35,900	2,500	95.60	4.00	0.40
1984	63,000	4,300	99.95	0.00	0.05
1985	64,600	4,500	99.93	0.00	0.07[2]
1986	50,500	4,100	99.98	0.02[3]	0.00
1987	71,090	4,400	99.96	0.04[4]	0.00
1988	91,800	5,680	>99.98	0.02[5]	0.00
1989	64,100	3,966	100.0	0.00	0.00

[1]Willard A. Dickerson, North Carolina Department of Agriculture, Raleigh, North Carolina.
[2]66 weevils in 3 fields
[3]1 weevil
[4]1 weevil in each of 2 fields
[5]9 weevils in 1 field

economic assessment indicates that the total benefits resulting from the program exceeded $75 per acre in both North Carolina and South Carolina (Carlson *et al.*, 1989). The southeastern program was expanded, beginning in 1983 (Figure 2). Pheromone traps continued to play a prominent role in detection, monitoring and suppression of boll weevil populations (Ridgway *et al.*, 1990b), with several hundred thousands of traps and several million pheromone dispensers being used annually.

An organized areawide boll weevil management/eradication program was initiated in southern California, southwestern Arizona and part of Mexico in 1985. Extensive trapping, insecticide applications and cultural controls led to elimination of reproducing populations in these areas by 1987 (National Cotton Council of America, 1989). In 1988, the program was expanded to cover the remainder of Arizona and adjoining areas of Mexico. In this southwestern program, the boll weevil pheromone trap was used primarily for detection and to aid in decision-making related to insecticide application (Anonymous, 1989). About 50,000 traps, deployed at one or two traps per 10 acres (4 hectare) and 1,200,000 pheromone dispensers were used in 1988 (Personal communication, Frank Myers, retired, Phoenix, Arizona).

PINK BOLLWORM

The pink bollworm is a serious pest of cotton in much of the western cotton growing region of the United States. Overwintering occurs by larvae within cotton seeds, bolls or plant remnants in the field or at the gin. Damage in the form of yield loss and reduction in quality occurs from larval feeding on seeds within green bolls. There may be as many as six generations each year in areas with long growing seasons.

Behavioral studies apparently played only a limited role in the discovery of the pink bollworm pheromone, since original studies utilized primarily empirical screening in an effort to discover attractants for the pink bollworm (Jacobson, 1969; Keller, 1969). However, efforts to confirm the presence of some of these attractants in the insect led to the discovery of the natural sex pheromone. The sex pheromone of the pink bollworm (Hummel *et al.*, 1973; Bierl *et al.*, 1974) is a 60:40 blend of the *Z,Z* and *Z,E* isomers of 7,11-hexadecadien-1-ol acetate.

The synthetic pheromone, gossyplure, is commercially formulated in a 50:50 mixture. It is currently used in traps for population surveillance, as a mating disruptant and, along with an insecticide, as an attracticide. The development and use of gossyplure in surveillance and suppression has been recently reviewed by Staten *et al.* (1988) and Baker *et al.* (1990). The quality of gossyplure used for monitoring and the development of different delivery systems for use in control programs are worthy of special note. However, since gossyplure is the only pheromone currently in use for control of a cotton insect by mating disruption, emphasis will be placed on this aspect. Use of gossyplure for control of the pink bollworm had its beginning with the landmark research of Shorey *et al.* (1976) and Gaston *et al.* (1977), utilizing a hollow-fiber dispensing system. Although these original experiments were criticized for the lack of untreated controls, they were responsible for launching a series of events over the next decade that has led to the widespread acceptance of gossyplure as a pink bollworm management "tool".

Although the original hollow-fiber dispensing system (NoMate® PBW) was approved for commercial use in the United States (Tinsworth, 1990) in 1978, uncertainty about its efficacy and difficulties with application hindered its acceptance. Then in 1982, following several years of declining yields and increased pesticide use, with its associated secondary pest problems, cotton growers in California's Imperial Valley established a Pest Abatement District that mandated at least four pheromone (gossyplure) disruption sprays. A total of 45,600 acres (18,226 hectares) was treated with gossyplure; insecticide use was postponed until later in the season. The program was successful in that average yields increased from 2.2 bales/acre (5.4 bales/hectare) in 1981 to 2.7 bales/acre (6.7 bales/hectare) in 1982, and secondary pest problems early in the season were greatly reduced. While the mandatory program was not continued, most growers voluntarily continued to use pheromone treatments the next year (Baker *et al.*, 1990).

Further evaluation of the hollow-fiber and laminate flake dispensing systems (Disrupt® PBW) and of a wire-reinforced sealed polyethylene tube (PB-ROPE®) (Table 2) (Staten *et al.*, 1987) and subsequent studies (Staten *et al.*, 1988) have led to

improved confidence in mating disruption. Although difficult to quantify, the use of the pheromone, gossyplure, with a toxicant in an attracticide approach has also had a significant impact (Baker *et al.*, 1990). A review of the percentage of acreage treated with gossyplure products from 1982 to 1986 reveals a trend towards increased uses of this pheromone, with the percentage of acreage treated increasing from 15 to 29 percent (Baker *et al.*, 1990). More recently, three different sprayable bead formulations (Checkmate® PBW, Decoy® PBW Beads and NoMate® PBW MEC) and another point-source dispenser (Decoy® PBW Stakes) have been developed (Brosten and Simmonds, 1990). Indications are that the number of acres treated with a pink bollworm pheromone-based product in 1990 substantially exceeded that treated in any previous year (Personal communication, Charles C. Doane, Scentry, Inc., Goodyear, Arizona).

In addition to the control programs in southern California and Arizona, the California Department of Food and Agriculture (CDFA) has also maintained an aggressive suppression/eradication program in the nearly 300,000 acres of cotton grown in the San Joaquin Valley. This is a cooperative program involving cotton producers, CDFA and USDA. When pink bollworm moths are detected by a grid of pheromone traps, the infested area is treated with releases of sterile males and with aerially applied gossyplure disruptant-attracticide (Baker *et al.*, 1990). This program is widely recognized as being successful in preventing establishment of pink bollworm populations in the San Joaquin Valley.

Table 2. Effects of PB-ROPE® treatment on pink bollworm damage (number of larvae in bolls) and insecticide use in the Imperial Valley of California and Mexicali Valley of Mexico in 1985. (From Staten *et al.*, 1987.)

Treatment	No. of fields	Pink bollworm Larvae/100 bolls August	Pink bollworm Larvae/100 bolls September	Average no. of insecticide treatments per field
	Imperial Valley[1]			
Conventional insecticide	8	0.85	0.88	11.4 a
Conventional pheromone	8	0.90	2.1	10.4 a
PB-ROPE pheromone	7	0.32	0.39	6.6 b
	Mexicali Valley[2]			
Conventional insecticide	14	1.72 a	1.55 a	4.9 a
PB-ROPE pheromone	16	0.7 b	0.72 b	2.9 b

[1]The eight conventional pheromone fields were treated with Nomate PBW® or Disrupt®. Means in same column having no letters in common are significantly different according to ANOVA followed by Duncan's multiple range test (P=0.01).

[2]Means in same column having no letters in common are significantly different according to Student's t test (P=0.01).

BOLLWORM AND TOBACCO BUDWORM

The world-wide *Helicoverpa/Heliothis* complex includes a number of major pests of agricultural crops. In the United States, two species from this group, the bollworm, and the tobacco budworm are among the most important insects attacking field crops, accounting for annual losses and costs for control of hundreds of millions of dollars (Sparks *et al.*, 1988). Crops damaged by these two insects include cotton, corn, beans, garden peas, peppers, tomatoes, lettuce, sorghum, alfalfa, clover, vetch, tobacco and peanuts (Davidson and Lyon, 1979). In cotton, the bollworm was recognized as an important pest as early as 1841 (Quaintance and Brues, 1905), while the tobacco budworm did not achieve prominence until much later (Sparks *et al.*, 1988). For some time, control was achieved by use of insecticides, but development of resistance to the chlorinated hydrocarbons, followed by the organophosphates and carbamates (Harris *et al.*, 1972), and more recently by the pyrethroids (Miller, 1985) has intensified the need for other methods for management of these two pests.

Both the bollworm and the tobacco budworm are nocturnal (active at night), so direct field observations of mating behavior were limited until the development of night-vision methodology (Lingren *et al.*, 1978). Field analysis of behavior also is difficult because of the tendency of the females to change locations and the often fierce competition between males for an individual female (Sparks *et al.*, 1988). Nevertheless, understanding of the behavior patterns and the interactions of the various influences affecting the bollworm and tobacco budworm is important in assessing the potential role of pheromones in the management of these insects. Most early behavioral studies involved laboratory-reared insects and/or laboratory or cage tests. In 1962 and 1963, Gentry *et al.* (1964) showed that traps baited with laboratory-reared female tobacco budworm moths or with extracts from the females captured released-male moths, thus demonstrating the presence of a sex attractant emitted by the females. Teal *et al.* (1981) reported details of the precourtship and courtship behaviors of male and female tobacco budworm moths in wind tunnel and cage tests.

Although the sex pheromones are the primary means of mating communication for the tobacco budworm and the bollworm, there is evidence that visual communication may be a supplementary short-range mate-detection mechanism (Sparks *et al.*, 1988). For example, male bollworm moths flying toward a cotton wick impregnated with a pheromone source were observed to move instead toward a mock female constructed of brown paper at distances of 6.3 to 8.7 inches (16 to 22 centimeters) (Carpenter and Sparks, 1982). The actual production of the pheromones is influenced by a number of external factors, including photoperiod and host plant (Raina, 1988). It is regulated internally by one or more neurohormones (Raina *et al.*, 1989a). Further, the role of host plant attractants and feeding stimulants should be recognized, since these materials could potentially be useful in suppression programs (Lingren *et al.*, 1990).

The chemistry of the pheromones of the bollworm/tobacco budworm complex has been reviewed by Sparks *et al.* (1988) and Lopez *et al.* (1990). Initial efforts to identify the pheromones of the bollworm and tobacco budworm were hampered by the lack

of adequate bioassays and the low sensitivity of analytical instrumentation and methodology. Thus, initial identifications were inaccurate or incomplete (McDonough *et al.*, 1970; Roelofs *et al.*, 1974; Tumlinson *et al.*, 1975). A number of subsequent studies were conducted with pheromone gland extracts. The presence and importance of multiple component mixtures—4 and 7 components from the pheromone glands of the bollworm and tobacco budworm, respectively—were reported by Klun *et al.* (1979) (Table 3). Subsequent studies of pheromone gland extracts yielded information on the pheromones of five additional species in the *Helicoverpa/Heliothis* complex (Table 3) (Sparks *et al.*, 1988). Although the components vary from species to species, *(Z)*-11-hexadecenal is the major pheromone component in all species of the complex that have been studied. There is considerable variation in the reported compositions of the pheromone blends for the different species. Differences associated with many factors can give rise to a substantial range in the numbers of components found or in the reported component ratios. These factors include: (a) methodology and the sensitivity of the analytical technique; (b) the source of the pheromone, whether from an extract or from emitted volatiles; (c) laboratory-reared vs. wild insects (Raina *et al.*, 1989b); (d) insect strains (Ramaswamy and Roush, 1986); and (e) individual variations among insects. Variation is also encountered in studies to determine the behavioral responses to the various pheromone components. Flight tunnel studies and field trapping studies do not always give comparable results. Data obtained are affected by many factors, such as the pheromone dispenser system, the trap design, the presence of host plants, and environmental conditions such as temperature.

With the tobacco budworm, the binary mixture of *(Z)*-11-hexadecenal and *(Z)*-9-tetradecenal (often referred to as virelure) is an effective trap lure, but the addition of *(Z)*-11-hexadecen-1-ol has been demonstrated to improve trap captures (Ramaswamy *et al.*, 1985; Shaver *et al.*, 1987). Lures containing this alcohol at a level of 0.25 to 1 percent of that of *(Z)*-11-hexadecenal gave optimum trap captures while higher levels of the alcohol suppressed captures. With the bollworm, a binary mixture of two C-16 aldehydes, *(Z)*-11-hexadecenal and *(Z)*-9-hexadecenal, is an effective trap lure, but there is some indication that the quaternary mixture of the four components identified for this insect (Table 3) is a more effective lure. Addition of *(Z)*-11-hexadecen-1-ol, which increased trap captures with the tobacco budworm, reduced captures of the bollworm when used with this four-component mixture (Teal *et al.*, 1984). Differences in the ratios of major components and the presence of various other components, often in trace quantities, seem to be responsible for pheromone specificity in these insects, although the roles of the individual components are not fully understood.

As with pheromones and other behavior-modifying chemicals of other insects, those associated with the bollworm and tobacco budworm theoretically could be used for surveillance or suppression. Research related to practical applications has been concentrated primarily on use of the sex pheromones (Sparks *et al.*, 1988; Lopez *et al.*, 1990). The availability of more complete pheromone blends raised the expectation that suppression with pheromones might be possible through mass trapping, mating disruption or use in attracticides. However, review of available information indicates

Table 3. Female pheromonal components for four species of *Heliothis* and three species of *Helicoverpa* determined by analyses of extracts of the pheromone glands. (Modified from Sparks *et al.*, 1988.)

Compound	Species of *Heliothis*				Species of *Helicoverpa*		
	virescens[1]	*subflexa*	*phloxiphaga*	*peltigera*[2]	*zea*[3]	*punctigera*[3]	*amigera*
	percent of total pheromone content						
(Z)-9-tetradecenal	2.0	0.2	-	9.2	-	-	-
tetradecanal	1.6	0.3	-	0.5	-	-	-
(Z)-9-tetradecen-1-ol	-	-	-	4.1	-	-	-
(Z)-9-tetradecen-1-ol acetate	-	-	-	1.3	-	-	-
(Z)-7-hexadecenal	1.0	2.0	-	0.7	1.1	-	-
(Z)-9-hexadecenal	1.3	15.1	0.5	0.9	1.7	-	3.0
(Z)-11-hexadecenal	81.4	40.5	91.8	62.8	92.4	60	87.0
hexadecanal	9.5	1.3	4.8	2.3	4.4	-	4.0
(Z)-11-hexadecen-1-ol	3.2	5.2	2.9	15.2	-	-	-
hexadecanol	-	-	-	-	-	-	6.0
(Z)-7-hexadecen-1-ol acetate	-	2.7	-	-	-	-	-
(Z)-9-hexadecen-1-ol acetate	-	6.2	-	-	-	-	-
(Z)-11-hexadecen-1-ol acetate	-	25.5	-	3.0	-	25	-
hexadecanol acetate	-	-	-	-	-	-	6.0

[1]*Heliothis virescens* = tobacco budworm; *Helicoverpa zea* = bollworm.

[2](Dunkelblum and Kehat, 1989)

[3](Rothschild *et al.*, 1982) Identification of pheromone components was not complete.

a number of major limitations. Mass trapping is limited by trap efficiency, which may vary from 3 to 55 percent, based on the percentage of males responding to the vicinity of a trap (Sparks *et al.*, 1979a, 1979b). Also, the most efficient traps are large and complicated, thus limiting their practical use in large numbers. Considerable research on mating disruption (or communication disruption) has been done with the bollworm and the tobacco budworm, but results are not promising (Sparks *et al.*, 1988). Reduction in mating was achieved in some studies, but it is questionable whether any practical reduction in populations can be achieved. The high mobility of the bollworm and tobacco budworm, with the consequent immigration into treated areas, and the role of vision in close-range orientation of males to females are factors that may prevent development of mating disruption into a viable means of bollworm/tobacco budworm control. Similarly, in tests of insecticidal baits laced with pheromones, satisfactory results were not obtained, even when a feeding stimulant was incorporated in the attracticidal bait, because contact of the insects with the insecticide in the bait was not sufficient to be of biological significance (Sparks *et al.*, 1988).

A number of plant products have been explored as feeding stimulants to enhance the efficacy of microbial agents against cotton bollworm and tobacco budworm larvae. At least one, derived from cottonseed flour, has shown enough promise to be commercially marketed (Stamps, 1981).

Because of the limited success in the use of pheromones for control of the bollworm and tobacco budworm, major research efforts in recent years have emphasized the use of pheromones in traps for monitoring populations. However, the large number of variables influencing trap capture and its relation to field infestations often complicates the practical use of traps. These many variables include the pheromone blend, the dispenser, trap design, characteristics of individual species and all the abiotic and biotic factors that influence the fate of the pheromone and the behavior, fecundity and mortality of the insect. The status of the development of dispensers and trap designs has been reviewed elsewhere (Lopez *et al.*, 1990), therefore, only some highlights will be provided here. Although a number of dispensers are available commercially, a plastic laminate dispenser for the bollworm pheromone and a black molded polyvinyl chloride dispenser for the tobacco budworm pheromone or its major components appear to be the dispensers of choice. Preliminary performance criteria have been developed for these dispensers (Leonhardt *et al.*, 1987). Of the many trap designs evaluated, the modified wire cone trap (Hartstack *et al.*, 1979) continues to be the preferred trap of researchers, although some alternatives are commercially available (Lopez *et al.*, 1990).

Pheromone-baited traps have been used in monitoring with at least four different objectives: (a) collection; (b) detection; (c) population estimation; and (d) prediction. Examples particularly worthy of note from those reviewed by Lopez *et al.* (1990) include: collection of insects to monitor the level of insecticide resistance in field populations (Plapp *et al.*, 1987); detection of bollworms near high-value crops; successful measurement of field populations (Hartstack *et al.*, 1978; Johnson, 1983; Witz *et al.*, 1985); and population prediction (Hartstack *et al.*, 1983; Witz *et al.*, 1985). It should

be emphasized that the results from the use of traps for population estimation and prediction have been highly variable, but research is continuing to reduce this variability. Therefore, with further refinements of pheromone trap inputs into population models to increase the accuracy of both timing and density of field populations, pheromone traps could become an invaluable tool in the management of the bollworm and tobacco budworm (Hayes and Coleman, 1989).

PLANT BUGS

Three *Lygus* species (Heteroptera: Miridae) that are pests of cotton are the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois), the pale legume bug, *Lygus elisus* Van Duzee, and the western lygus bug, *Lygus hesperus* Knight. These bugs cause shedding of cotton squares and young bolls by puncturing and feeding with their piercing-sucking mouth parts. Older bolls may be damaged but are less likely to be shed. Scales (1968) observed that caged female tarnished plant bugs attract males. Subsequent findings have shown that this also occurs with other mirids (Aldrich, 1988a, 1995). This attraction is temporarily lost upon mating. Male tarnished plant bugs, as well as a few males of other mirid species, were captured in traps baited with virgin females (Slaymaker and Tugwell, 1984). Cross attraction of males by females occurred between the tarnished plant bug and the pale legume bug, but western lygus bug males were attracted only by conspecific females (e.g., females of the same species) (Graham, 1987). The source of the attractive material has not been determined.

A variety of compounds have been identified in volatile material from females of these three *Lygus* species (Aldrich, 1988a), including a number of acetates, butyrates and other aliphatic esters, as well as *(E)*-2-hexenal, *(E)*-4-oxo-2-hexenal and *(E)*-hexenol. As yet, no significant attraction to any combination of these compounds has been demonstrated (Aldrich, 1988a, 1995), although traps baited with virgin female tarnished plant bugs have been used for monitoring (Slaymaker and Tugwell, 1984). Elucidation of the attractive compounds would provide more efficient trapping methods and improved management of these pests.

PHYTOPHAGOUS STINK BUGS

Phytophagous (plant feeding) stink bugs such as the southern green stink bug, *Nezara viridula* (L.) (Heteroptera: Pentatomidae), are occasional pests of cotton. Mitchell and Mau (1971) noted that adult males of this insect were attractive to virgin females in olfactometer and field tests. Subsequently, it was shown that males and nymphs of the southern green stink bug also were attracted to males in the field (Harris and Todd, 1980). Aldrich *et al.* (1987) demonstrated that males emitted a volatile material that was attractive to adult insects and nymphs in the field. The site of production of this pheromone has not been determined. It appears that this aggregation pheromone serves as a long-range attractant for mate location but is not involved in close-range courtship (Todd, 1989). Numerous male-specific compounds, including *(Z)*-a-bisabolene [*(Z)*-1-methyl-4-(1,5-dimethyl-1,4-hexadienyl)cyclohexene] and *cis* and *trans-(Z)*-a-bisabolene epoxides, have been identified from male-produced air-

borne volatile material (Figure 3) (Aldrich, 1995; Baker *et al.*, 1987). Some of these compounds have been shown to be attractive to females in laboratory bioassays (Aldrich, 1988a). Southern green stink bugs from different geographic locations produce pheromone blends with different ratios of major components, indicating the existence of different strains of the insect (Aldrich *et al.*, 1989). Tests have not established which of these compounds are required for pheromonal activity in the field (Aldrich, 1995). Volatiles from males of another occasional pest of cotton, the green stink bug, *Acrosternum hilare* (Say), contain many of the same components isolated from the southern stink bug, but there are marked differences in the relative abundance of some of these components (Aldrich *et al.*, 1989). When the male-specific compounds required for field attraction of these phytophagous pentatomids have been determined, they should be useful in traps for monitoring populations (Aldrich, 1988b).

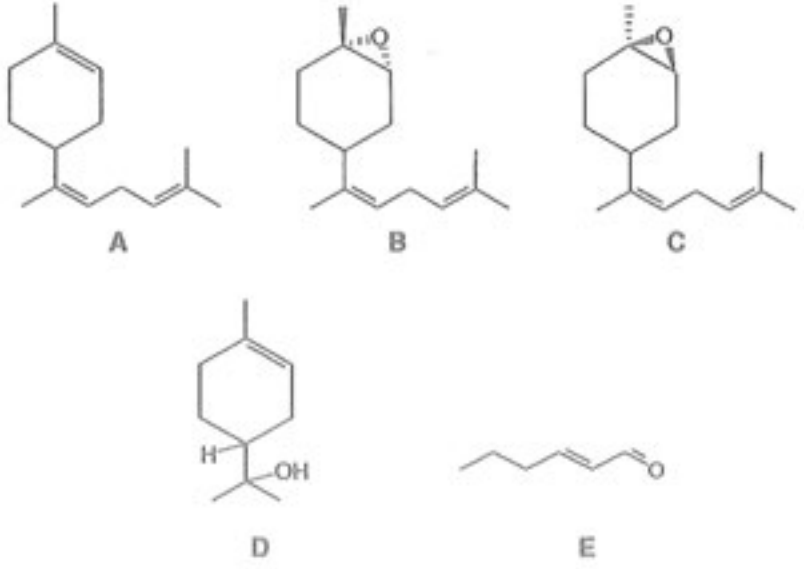


Figure 3. Primary components of pheromones of the pentatomids, southern green stink bug (A, B), green stink bug (A, C), and spined soldier bug (D, E). A, *(Z)*-a-bisabolene; B, *trans-(Z)*-a-bisabolene epoxide; C, *cis-(Z)*-a-bisbolene epoxide; D, (+)-*R*-a-terpineol; E, *(E)*-2-hexenal ("leaf-aldehyde") (Modified from Aldrich, 1995).

PHYTOPHAGOUS MITES

Spider mites (Acari: Tetranychidae) often become a problem in cotton when insecticides kill the predator insects and mites that regulate their numbers. The twospotted spider mite, *Tetranychus urticae* Koch, is widely distributed. It feeds on many hosts and perhaps is the most abundant species on cotton. At least 32 additional species of tetranychid mites are reported to be pests of cotton (Leigh, 1985).

Ewing (1914) first recorded the observation that male twospotted spider mites were attracted to quiescent (inactive) females prior to their final molt and remained nearby until the adult females emerged, at which time mating occurred. Cone *et al.* (1971a, 1971b) showed that extracts of the deutonymphs were attractive to males in laboratory bioassays. Further studies (Penman and Cone, 1972, 1974) demonstrated that tactile (sense of touch) stimuli from the web produced by the female deutonymphs played a role in the attraction of males and that the volatile material was a short-range attractant or an arrestant that maintains male interest in the female.

Regev and Cone (1975, 1976) identified the sesquiterpene alcohol, farnesol (3,7,11-trimethyl-2,6,10-dodecatrien-1-ol), as the attractive material in extracts of quiescent female twospotted spider mites; the *Z,E* isomer was more attractive than the *Z,Z* isomer. Another sesquiterpene alcohol, nerolidol (3,7,11-trimethyl-1,6-10-dodecatrien-3-ol), found in the extract also showed attractancy. Subsequently, a monoterpene alcohol, citronellol (3,7-dimethyl-6-octen-1-ol), was identified from pharate females and was highly attractive to males in bioassays (Regev and Cone, 1980).

Because it is an arrestant or short-range attractant, the pheromone would not be effective in attracting the mites to monitoring traps. However, a mixture of *(Z,E)*-farnesol and nerolidol, under the trade name Stirrup-M®, was approved for commercial use (Tinsworth, 1990) in 1987 as a selective mite pheromone for use against the twospotted spider mite; the carmine spider mite *Tetranychus cinnabarius* (Boisduval); other *Tetranychus* species; and the European red mite, *Panonychus ulmi* (Koch). It is intended to be mixed with a conventional miticide to increase the time mites remain on treated crop surfaces, thereby increasing the efficacy of the miticide and making it possible to reduce the quantities used and the frequency of applications.

PARASITES AND PREDATORS

A variety of behavior-modifying chemicals influence the actions of beneficial insects in cotton, and the interactions of these factors are very complex (Jones *et al.*, 1976). Consequently, identification of specific chemicals has proceeded slowly. Sex pheromones have been demonstrated for a few parasites and predators, and some parasites have been shown to deposit marking pheromones that prevent repeated searches over the same area or that prevent superparasitiztion. Pheromones or other substances from the host insect frequently are found to serve as kairomones, stimulating the parasite or predator to search for a host or serving as an attractant. In addition to these chemicals from the parasite or predator and from its host or prey, cues from the preferred habitat of the host also affect the behavior of beneficial insects. Phytochemicals from the host's food plant may serve as attractants or stimulants.

The phenomenon of "learning" is another unique characteristic encountered in the study of these behavioral chemicals. Frequently, exposure of a parasite to a host or to host-derived kairomones increases the efficiency of searching for other hosts. This "success-motivated searching" (Vinson, 1977) must be considered in designing experimental studies on applications of behavior-modifying chemicals of beneficial insects.

Various types of behavior-modifying chemicals, primarily kairomones, have been reported for a wide range of natural enemies of pests associated with cotton. Some examples are summarized in Table 4. The natural enemies listed in the table include: parasites that attack eggs (four genera), larvae (five genera) and adults (one genus); and four genera of predators. Some of these natural enemies are host-specific, while others attack a wide range of hosts. The hosts listed in Table 4 are generally those reported in the references cited.

EGG PARASITES

The behavioral chemicals affecting egg parasites include various kairomones left by ovipositing lepidopterous host females. With *Trichogramma pretiosum* Riley, for example, bollworm moth scale extracts increased parasitization, apparently by stimulating increased searching (Jones *et al*., 1976). From bollworm scale extracts, Jones *et al*. (1973) identified four straight-chain hydrocarbons having kairomonal activity for *Trichogramma evanescens* Westwood; of these, tricosane was the most active. Increased rates of parasitization of bollworm eggs were also observed with *Trichogramma achaeae* Nagaraja and Nagarkatti after exposure to tricosane (Gross *et al*., 1975). Although *Trichogramma pretiosum* responded similarly to the bollworm moth scale extracts, tricosane produced no significant response with *Trichogramma pretiosum*, and while dotriacontane increased parasitism, it has not been shown to be present in moth scales (Jones *et al*., 1976).

Another type of kairomone, which is present in material from the accessory gland of female bollworm moths, stimulated ovipositor probing by *Trichogramma pretiosum* (Nordlund *et al*., 1987). Two proteins from the accessory gland of female tobacco budworm moths, apparently involved in adhesion of eggs, serve as egg recognition kairomones for *Telenomus heliothidis* Ashmead. Glass beads coated with these proteins were examined and probed by the parasite (Strand and Vinson, 1983). This recognition kairomone induced the parasite to oviposit and develop in nonhost eggs (Strand and Vinson, 1982), which could prove useful in artificial rearing of such parasites.

Pheromones of the host insect can also serve as kairomones. Gossyplure, the synthetic pheromone of the pink bollworm, caused increased parasitization of pink bollworm eggs by *Trichogramma pretiosum* (Zaki, 1985). The synthetic pheromone blend of the bollworm increased rates of parasitization of the bollworm eggs by this same parasite (Lewis *et al*., 1982; Noldus, 1988).

Searching or ovipositing parasites leave marking pheromones around or within the host eggs (Salt, 1937; Gardner and van Lenteren, 1986; Okuda and Yeargan, 1988). These marking pheromones increase the efficiency of searching and reduce superparasitiztion.

LARVAL AND ADULT PARASITES

As with the egg parasites, kairomones from the host affect the behavior of larval parasites. Mixtures of methyl-branched hydrocarbons that stimulate searching of *Cardiochiles nigriceps* Viereck, *Microplitis croceipes* (Cresson) and *Microplitis*

Table 4. Behavior-modifying chemicals affecting parasites and predators of cotton pests.

Insect	Host	Source and/or stimulus	Action	Reference
EGG PARASITES (Hymenoptera: Trichogrammatidae)				
Trichogramma achaeae	bollworm	moth scales, tricosane and other hydrocarbons	search stimulating kairomone	(Gross *et al.*, 1975)
Trichogramma evanescens	bollworm, wide range of hosts	moth scales, tricosane and other hydrocarbons	search stimulating kairomone	(Jones *et al.*, 1973)
		odors from another female *T. evanescens*	marking pheromone	(Salt, 1937)
		host egg	arrestment (contact pheromone)	(Gardner and van Lenteren, 1986)
	pink bollworm	host sex pheromone (gossyplure)	kairomone, increased parasitization	(Zaki, 1985)
Trichogramma pretiosum	bollworm, other moths	moth scale extracts	search stimulating kairomone	(Jones *et al.*, 1976)
		accessory gland of female bollworm	oviposition stimulating kairomone	(Noedlund *et al.*, 1987)
		bollworm pheromone	host seeking kairomone	(Lewis *et al.*, 1982, Noldus, 1988)
EGG PARASITES (Hymenoptera: Scelionidae)				
Telenomus heliothidis	tobacco budworm	tobacco budworm eggs (two proteins)	host egg recognition kairomone	(Strand and Vinson, 1983)
Telenomus podisi	pentatomids	female parasite on parasitized eggs	host egg marking pheromone	(Okuda and Yeargan, 1988)
Trissolcus euschisti	pentatomids	female parasite on parasitized eggs	host egg marking pheromone	(Okuda and Yeargan, 1988)
EGG PARASITES (Hymenoptera: Braconidae)				
Chelonus curvimaculatus	pink bollworm	moth scales	search stimulating kairomone	(Chiri and Legner, 1982)
LARVAL PARASITES (Hymenoptera: Ichneumonidae)				
Campoletis sonorensis	tobacco budworm	cotton plant	attractant and search stimulating synomones	(Elzen *et al.*, 1984a)
		female Dufours gland	host marking pheromone	(Guillot and Vinson, 1972)
		female oviducts (water soluble material)	oviposition deterrent pheromone	(Guillot and Vinson, 1972)
LARVAL PARASITES (Hymenoptera: Braconidae)				
Bracon mellitor	boll weevil	frass (diet-specific component)	oviposition probing stimulant	(Vinson *et al.*, 1976)
Cardiochiles nigriceps	tobacco budworm	larval mandibular gland, frass, methyl-branched hydrocarbons	host-seeking stimulant kairomone	(Vinson *et al.*, 1975)
		female in cocoon	short-range sex pheromone	(Vinson, 1978)
		female Dufours gland (unidentified hydrocarbons)	host marking pheromone	(Guillot *et al.*, 1974)

Table 4. Continued.

Insect	Host	Source and/or stimulus	Action	Reference
Microplitis croceipes	bollworm	frass hydrocarbons, 13-methylhentriacontane	host-seeking stimulant kairomone	(Jones *et al.*, 1971)
		plant compounds in larval frass increased	host searching	(Nordlund and Sauls, 1981)
		female Dufours gland	host-marking pheromone	(Vinson and Guillot, 1972)
		females	sex attractant pheromone	(Elzen and Powell, 1988, 1989)
Microplitis demolitor	bollworm	frass hydrocarbons, 13-methylhentriacontane	host-seeking stimulant kairomone	(Nordlund and Lewis, 1985)
LARVAL PARASITES (Diptera: Tachinidae)				
Archytas marmoratus	tobacco budworm	larval, frass (in most noctuid larvae) (a protein)	larviposition stimulant kairomone	(Nettles and Burks, 1975)
ADULT PARASITE (Diptera: Tachinidae)				
Trichopoda pennipes	southern green stink bug	male host pheromone	attractant kairomone	(Mitchell and Mau, 1971)
PREDATORS (Neuroptera: Chrysopidae)				
Chrysoperla carnea	bollworm	moth scales	search stimulant kairomone	(Lewis *et al.*, 1977)
		accessory gland secretion (egg adhesive)	prey acceptance kairomone	(Nordlund *et al.*, 1977)
		b-caryophyllene from cotton	attractant synomone (for adults)	(Flint *et al.*, 1979)
PREDATORS (Coleoptera: Malachiidae)				
Collops vittatus	large variety of insects	caryophyllene oxide from cotton	attractant in traps	(Flint *et al.*, 1979)
PREDATORS (Heteroptera: Pentatomidae)				
Podisus maculiventris	large variety of insects	males, a-terpineol and *(E)*-2-hexenal	sex attractant pheromone	(Aldrich *et al.*, 1984)
PREDATORS (Acari: Phytoseiidae)				
Phytoseiulus persimilis	tetranychid mites	mites on plants	attractant kairomones	(Sabelis and Dicke, 1985)

demolitor Wilkinson have been identified from frass (excrement) or larvae of the tobacco budworm (Vinson *et al.*, 1975) and the bollworm (Jones *et al.*, 1971; Nordlund and Lewis, 1985), respectively; 13-methylhentriacontane was one of the more active components. A proteinaceous material found in the frass or hemolymph of most noctuid larvae stimulates larviposition (deposition of living larvae) in the tobacco budworm larva by the tachinid parasite *Archytas marmoratus* (Townsend) (Nettles and Burks, 1975). Also, the pheromone of the male southern green stink bug is a kairomone that attracts the parasite *Trichopoda pennipes* (F.) (Mitchell and Mau, 1971, Todd and Lewis, 1976).

Like the egg parasites, larval parasites also employ marking pheromones. Vinson and Guillot (1972) demonstrated that material from the Dufours gland permits *Microplitis croceipes*, *Cardiochiles nigriceps* or *Campoletis sonorensis* (=*perdistinctus*) (Cameron) to distinguish between nonparasitized and parasitized larvae of the tobacco budworm. The existence of sex pheromones in some parasites has also been demonstrated. Vinson (1978) presented evidence for a short-range pheromone emitted by females while still in the cocoon. Elzen and Powell (1988) have reviewed the evidence for a volatile sex pheromone emitted by female *Microplitis croceipes*; they have shown that male *Microplitis croceipes* can be caught in traps baited with virgin females.

Parasites also are affected by chemical cues originating from the habitat frequented by their hosts. These chemicals are classed as synomones since they facilitate location of the host by the parasite and are therefore of mutual benefit to the parasite and the host plant. Williams *et al.* (1988) have reviewed such parasite—plant interactions, with particular reference to cotton and to *Campoletis sonorensis*. *Campoletis sonorensis* females have been shown to orient to and search cotton plants that are host-free (Elzen *et al.*, 1983); in this case, both volatile and contact chemicals were involved. Certain compounds from cotton that are attractive to *Campoletis sonorensis* are not found in larval frass from diet-reared tobacco budworm larvae, but feeding cotton to diet-reared larvae increased the kairomonal activity of the larvae and their frass (Elzen *et al.*, 1984b). Similarly, in laboratory experiments, *Microplitis croceipes* females responded to the extracts of frass from bollworm larvae reared on cotton, but not to frass from larvae reared on corn. This lack of response was shown to be the result of the absence of some chemicals in the corn (Nordlund and Sauls, 1981).

PREDACEOUS INSECTS

Predators respond to many of the same types of chemical cues as do the parasites. The rate of predation by the common green lacewing, *Chrysoperla carnea* (Stephens), on eggs of the bollworm was increased when bollworm moth scales or extracts of the scales were applied to the search area (Lewis *et al.*, 1977). Another kairomone for lacewing larvae appears to be present in the accessory gland secretion of the bollworm that causes adhesion of eggs to leaves (Nordlund *et al.*, 1977). The authors suggest that the scale kairomone is a search stimulant while that in the accessory gland secretion is involved in prey acceptance. A compound in cotton, *b*-caryophyllene, is attrac-

tive to adult female green lacewings, while another predator, *Collops vittatus* Say, a beetle, is caught in traps baited with caryophyllene oxide, another compound found in cotton (Flint *et al.*, 1979).

With the spined soldier bug, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae), which preys upon a large variety of insects and is the most widespread pentatomid predator in the United States, it has been demonstrated that males call a mate with pheromone from dorsal abdominal glands that open just under the wings. Females, males and immature nymphs respond to calling males. Although six compounds have been identified in volatiles from the male dorsal abdominal glands (Aldrich *et al.*, 1978), only two compounds are necessary for long-range attraction: (+)-*R*-a-terpineol and (*E*-2-hexenal. The compound (-)-*R*-a-terpineol has no adverse affect on attractancy so the cheaper racemic a-terpineol can be used for trapping (Aldrich, 1995).

A number of parasites and predators of the spined soldier bug were caught on or near traps baited with live males or with the synthetic pheromone of the spined soldier bug (Aldrich, 1985). These included the tachinid flies, *Hemyda aurata* Robineau-Desvoidy and *Euclytia flava* (Townsend); an ectoparastic biting midge, *Forcipomyia crinita* Saunders; two species of scelionid egg parasitoids, *Telenomus calvus* and *Telenomus podisi* Ashmead; and eastern yellowjackets, *Vespula maculifrons* (Buysson).

In addition to the use of the synthetic pheromone of the spined soldier bug for monitoring population levels of the predator, it has been suggested (Aldrich *et al.*, 1984) that it might be useful for: (a) luring these predators to pest infestations; (b) establishing them in areas where they are not now present; (c) moving them out of fields before applying an insecticide; or (d) assessing potential rates of parasitism.

PREDACEOUS MITES

Predatory phytoseiid mites such as *Phytoseiulus persimilis* Athias-Henriot prey upon spider mites. In an extensive review, Sabelis and Dicke (1985) summarize the many experiments demonstrating that prey location by these mites is facilitated by kairomones that may be prey-specific or may be derived from the host plant. The nature and chemical composition of these kairomones have not been elucidated.

OPPORTUNITIES

The highly successful use of the boll weevil pheromone in traps and the pink bollworm pheromone in mating disruption or attracticides should provide considerable impetus for exploiting opportunities for expanding the practical use of pheromones and other behavior-modifying chemicals in cotton pest management. Further, the ever-increasing need to reduce insecticide use and insect control costs provides strong justification to continue and expand research and development activities. The past successes have been associated with diverse research and development efforts involving chemistry, behavior, population ecology and delivery systems. Future successes undoubtedly

will require similar efforts. As attempts are made to manipulate more complex systems, increased emphasis should be placed on strategy definition and scientific integration.

Existing control technologies clearly will benefit from further refinements, and additional attention to development of new and improved pheromone-based surveillance methods will lead to additional practical uses. However, in terms of population suppression, future major advances may be associated with allelochemicals. The plant-derived kairomones for pests, such as attractants and feeding stimulants, often have the advantage of being active against both sexes, while the pheromones often are sex-specific. For this reason, the potential for suppression of the bollworm and tobacco budworm may rest with plant-derived chemicals, since movement of mated females clearly limits the use of pheromones for mating disruption. Additionally, fundamental new knowledge on hormonal regulation of pheromone production in Lepidoptera could lead to entirely new methods of disrupting the mating process (Ridgway *et al.*, 1990c).

Kairomones for natural enemies continue to be a very fertile field for research, for much is still to be learned. However, if this area of research is to have practical impact in the foreseeable future, major efforts on one or more model systems are needed, with a focus on the identification of useful chemical compounds and of the specific natural enemies to be manipulated.

SUMMARY AND CONCLUSION

Aggregation and/or sex pheromones have been identified and are in practical use for surveillance and/or suppression of the boll weevil, pink bollworm, cotton bollworm, and tobacco budworm. Boll weevil pheromone traps are used for surveillance related to the management of insecticides for overwintered boll weevil control in most areas of the United States where the boll weevil occurs. They are used as integral components of a number of areawide management programs. Boll weevil traps are used most intensively for both surveillance and suppression in the six states in the Southeastern Boll Weevil Eradication Program. The pink bollworm pheromone is used in the western United States for both surveillance and suppression; suppression is accomplished through mating disruption or use of attracticides, rather than mass trapping. The pheromones for both the bollworm and tobacco budworm are used primarily for monitoring in research programs. However, there is some commercial use, including the use of pheromone traps to sample tobacco budworms as part of a cooperative insecticide resistance management program.

The existence of sex pheromones in *Lygus* spp. has been demonstrated under field conditions by using live insects in traps as the source of the chemicals. The elucidation of the specific pheromone is complicated by the production in the scent glands of behavioral chemicals that are not attractants. Therefore, the chemical identities of the pheromones are not yet known. Pheromones of phytophagous stink bugs that attack cotton are known, as are pheromones for phytophagous mites. The latter pheromones are available commercially and are used to enhance the efficacy of miticides.

Chemicals produced from both insects and plants have been demonstrated to influence the behavior of natural enemies of cotton insects. The potential exists for utilizing these chemicals in a program involving mass rearing, pre-release behavioral modification and field behavioral manipulation to consistently provide adequate levels of pest protection.

Finally, in view of the selectivity of pheromones and other behavior-modifying chemicals, markets are often small and the incentives for private investment are limited. Also, expensive large-scale experimentation over a period of several years is often necessary to demonstrate efficacy and to develop practical management programs. Therefore, to take advantage of future opportunities, close cooperation between the public and private sectors, with a major resource commitment by the public sector, is essential.

AUTHORS' NOTE

The literature review for this chapter was essentially completed in July 1990. Some of the important events since that time include substantial advancement of the Southeastern Boll Weevil Eradication Program, development of improved formulations of gossyplure for use in suppression of the pink bollworm, and evaluation of the boll weevil bait stick for use in suppression of the boll weevil.

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Chapter 12

STATUS OF REARING TECHNOLOGY FOR COTTON INSECTS

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INTRODUCTION

Many insect pests of cotton can be cultured on synthetic diets in controlled environments to conduct research for development of advanced pest control concepts. Pest species with defined rearing procedures include: the boll weevil, *Anthonomus grandis grandis* Boheman (Coleoptera: Curculionidae); tobacco budworm, *Heliothis virescens* (F.) (Lepidoptera: Noctuidae); bollworm (corn earworm, tomato fruitworm), *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae); pink bollworm, *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae); plant bugs, *Lygus* spp. (Heteroptera: Miridae); and armyworms, *Spodoptera* spp. (Lepidoptera: Noctuidae). Certain beneficial species also can be reared on a large scale.

Diet formulations and rearing methods (manual vs. mechanical) for insect propagation are variable depending on production levels needed. These methods are described in recent literature. King and Leppla (1984) discuss colony establishment and maintenance through genetic control, diets and containers, engineering requirements for facilities, sanitation and microbial controls, quality control testing, systems management and descriptions of rearing techniques for specific insects. Singh and Moore (1985a,b) developed a set of "cookbook-style" handbooks in which specific instructions are given in a step-by-step manner for each operation in a particular rearing procedure. A worldwide listing of arthropod species in culture was published by Edwards *et al.* (1987) who cited contacts for many research programs. This work may be helpful when seeking insects for studies or for starting a colony. Rearing equipment ranging from bioclimatic chambers to large-scale facilities also have been described (Leppla and Ashley, 1978). More recently, Fisher and Leppla (1985) emphasized multi-room facilities for rearing Lepidoptera.

The ability to rear large numbers of insects must be integrated with a strategy for maintaining production and product quality control. A strong quality control component is crucial to any rearing program to ensure production output is maintained and that test or release insects will perform effectively. Laboratory-reared insects may become so strongly adapted to artificial rearing conditions that the information gained from experiments may be meaningless. The goals of this chapter are to describe: (a) the status and increased potential for applied biological control programs due to new technology available for insect rearing; (b) challenges that face entomologists in developing and employing effective biological control programs (production/release); (c) field evaluation technology for laboratory-reared insects; and, (d) a system for transferring new methodology to other agencies, to industry or to other potential users. Much of the discussion for the latter three goals will relate to boll weevil production.

STATUS OF REARING FOR MAJOR PESTS

The composite effect of advanced technology in insect rearing by refinements of defined diets and applied field programs have fostered development of engineering systems capable of meeting the challenges of today's biological control programs. Biological control is used broadly here to include use of sterile insects, backcross hybrids, etc. Future insect control concepts must be effective, economical and environmentally safe. The technologies needed are well developed and available through commercial sources. The necessary support and operational expertise are needed to put them into use.

The thermoform tray preparation technique introduced by Ignoffo and Boening (1970) and advanced by Sparks and Harrell (1976), who used a flash sterilizing unit (Figure 1) to process and deliver sterile diet to a thermoforming packing unit (Figure 2), established a prototype system that is adaptable to production of many insect species. The USDA, Agricultural Research Service (ARS), Southern Insect Management Laboratory, Insect Rearing Research Unit is housed in the R. T. Gast Rearing Laboratory at Mississippi State, Mississippi. Personnel of the Insect Rearing Research Unit have refined the system. They developed accessory tray assembly equipment that can be sanitized to deliver sterile diets to specialized trayforms for filling with diet and eggs. The eggs can be introduced in liquid or dry media, and diluted or concentrated for delivery to feeding cavities in desired quantities.

The mechanized system offers advantages desirable for mass production programs. Major advantages include improved sanitation control, reduced labor and increased production output capability. Commercial engineering firms with expertise for packaging specialized food and drug items have developed the basic technology to meet specialized operational requirements. The advantages gained through mechanized industrial insect production open the door for advanced use of pathogen-free insects for suppression programs, production of carcasses for specific virus and bacterial propagation, and mass rearing of host/prey insect species to culture predators and parasites for control of target pest species. Mechanized systems offer potential for expanded

Figure 1. Flash sterilizer for diet processing.

Figure 2. Thermoforming packaging unit to form and assemble rearing trays.

production with minimal stresses to personnel conducting program operations, compared to stress with expansion of rearing processes that require a high level of manual procedures.

Rearing procedures and equipment are available for mechanized production of the boll weevil, tobacco budworm, bollworm and the parasite *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae). A methods development program is in progress to adapt pink bollworm rearing operations to a mechanized process using flash sterilization and thermoform packaging units to meet the increasing needs for sterile release programs in California. The technical advancements gained by adapting insect rearing to packaging systems that can be managed sanitarily with a minimal labor force has advanced biological control concepts to the threshold of a new era. In order to better utilize and implement these technologies, personnel involved in research and field applications must review traditional problems with consideration of the changing times and advantages that different approaches to problems could yield. We must realize that mass production of insects is rational and presents a realistic solution to the complex problems introduced to today's agriculture.

BOLL WEEVIL REARING

In 1966, Gast and Davich described boll weevil colonization adapted to mass production processes, and technological advances continue to be made by USDA's, Insect Rearing Research Unit at Mississippi State, Mississippi. The Gast Laboratory opened in May, 1972 and produced 2.7 million sterile male boll weevils in 1973 for release in the Pilot Boll Weevil Eradication Experiment (Lindig, 1976). Major problems were encountered with microbial contamination of the diet and production costs due to intense labor requirements, especially in sexing the laboratory-reared weevils. In 1975, an Anderson 18-B Thermoforming packaging unit with prototype equipment designed for assembly of boll weevil trays was transferred from the USDA, ARS, Insect Migration/Dispersal Research Unit. In 1976, the first large-scale rearing program using the thermoforming packaging equipment was conducted. Production was 600,000 weevils per day for a six-week period. They were used as one of the technology components being tested in support of the proposed Boll Weevil Eradication Program. In 1977, a more ambitious program was conducted. Production averaged approximately 850,000 adults per day for a nine-week period. A fractionated pupal irradiation sterilization process was evaluated. During this period, problems were confronted concerning low egg production and microbial contamination of rearing trays.

Large-scale operation rearing procedures were critiqued during this period for procedural improvements and labor reduction. As a result, the following major modifications were implemented: (a) installation of High Efficiency Particulate Air (HEPA) filters in holding-room areas and within the chilling tunnel of the tray-forming unit; (b) use of sterile sand-corncob mix with antibiotics and fungicide for rearing trays; (c) modification of egg spray equipment for improved spray pattern on rearing trays; (d) change of glue formulation on Tyvek® lidding for improved seal; (e) improved environmental controls in holding room areas; (f) emergence of adults from trays to light

traps for collection; (g) feed-out of preirradiated adults in mosquito net bags; and, (h) use of rackveyors for holding rearing trays. The rearing procedures introduced from 1976-1979 were expected to improve field performance of sterile weevils by extending their longevity and improve the likelihood of eradicating low density field populations of weevils.

Photographs and descriptions of the facility and production equipment were detailed by Griffin (1984). The historical development of boll weevil diets was traced by Lindig (1984), and phases of laboratory rearing by Roberson (1984); microbial contamination was described by Sikorowski (1984).

Field data did not indicate increased pest control effectiveness that was anticipated from sterile weevils that were produced with the improved rearing methods. In 1984, survey tests were conducted at the rearing laboratory to observe weevil behavior (flight, walk, mating, etc.) following standard irradiation treatment processes. Investigations conducted in 1984 to 1985 by personnel at the Insect Rearing Research Unit and the USDA, ARS Boll Weevil Research Laboratory, Mississippi State, Mississippi (Roberson and Villavaso, 1986) observed high weevil mortality when aerial releases of weevils were made on soil surface temperatures reaching 120F (49C) and higher. Losses were also high if packaged weevils were stored for two or more days before release.

Studies in cooperation with USDA's, Animal and Plant Health Inspection Service (APHIS), Aircraft Operations Center, Mission, Texas, led to design and construction of paper tube loading equipment (Figure 3) to package irradiated weevils in paper cylinders for aerial dispersal. The improved handling and packing processes were evaluated in field releases in North Carolina in 1985 and in Alabama in 1987 and 1988. Noticeable improvement in the condition of shipped adult weevils resulted from use of the modified handling procedures. However, results obtained did not indicate sufficient control to justify incorporation of the sterile weevil concept in the ongoing Boll Weevil Eradication Program. The survey did provide valuable insight into essential considerations for future insect control programs. Shipping, holding and release methods employed for insects were recognized as being essential considerations. They are prime factors that determine establishment of released insects in the field, thus, the ultimate success of biologically-based control. This action (delivery) is analogous to proper application of insecticide in order to obtain expected field results. The same principle holds true with application of insects as insecticides—if released insects are not established in the field for any reason (poor quality, release technique), then control of target pests cannot be expected.

Present rearing capabilities at the Insect Rearing Research Unit were demonstrated during the 1987 and 1988 Alabama Sterile Boll Weevil Release Test (Powell *et al.*, 1988; Powell and Roberson, 1989). Powell *et al.* (1988) reported improved production capabilities resulted from: (a) adding beta-carotene to the diet; (b) collecting adult weevils in a chilled environment [54 to 59F (12 to 15C)]; (c) using large cages for adult feed-out; (d) using a diflubenzuron (Dimilin®) water dip treatment; and, (e) careful handling of packaged weevils in aerial release processes.

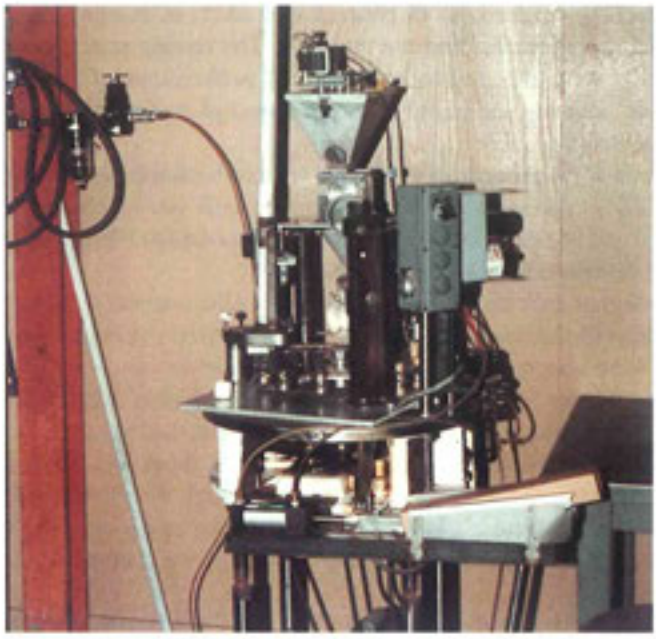

Figure 3. Boll weevil tube loader.

Powell and Roberson (1989) reported that 21.2 million weevils were produced in 1988 with 13.5 million irradiated for release. They also reported production output, operational requirements of materials and labor, and cost per 1,000-weevil rearing unit. More recently, data indicate that irradiation of emerging weevils in rearing trays (Figure 4) can significantly increase longevity of sterile weevils and reduce production costs by approximately 50 percent. The process utilizes the flash sterilizer/tray packaging system for mass production of microbe-free insects. The emerging weevils then are irradiated in the rearing trays and these trays are shipped directly to the field for release. This substantially reduces handling work operations of adult collection and packaging. Also, shipment of treated weevils in rearing trays that contain diet in moist conditions reduces critical stress encountered with previous shipping methods. The mechanized process offers advantages for each phase of the operational system and proposes a basic prototype that can be adapted to other insect species.

More recently, boll weevil mass rearing has been utilized to provide host food (Figure 5) for propagation of *Catolaccus grandis* (Burks) an ectoparasite that attacks third instar boll weevil larvae infesting cotton squares. Such rearing technology is a critical component of research development and field assessment.

Boll weevils are reared at other locations using various techniques. However, through a program organized by and operated through The Cotton Foundation, many public and private groups obtain weevils for testing purposes from the Gast Laboratory.

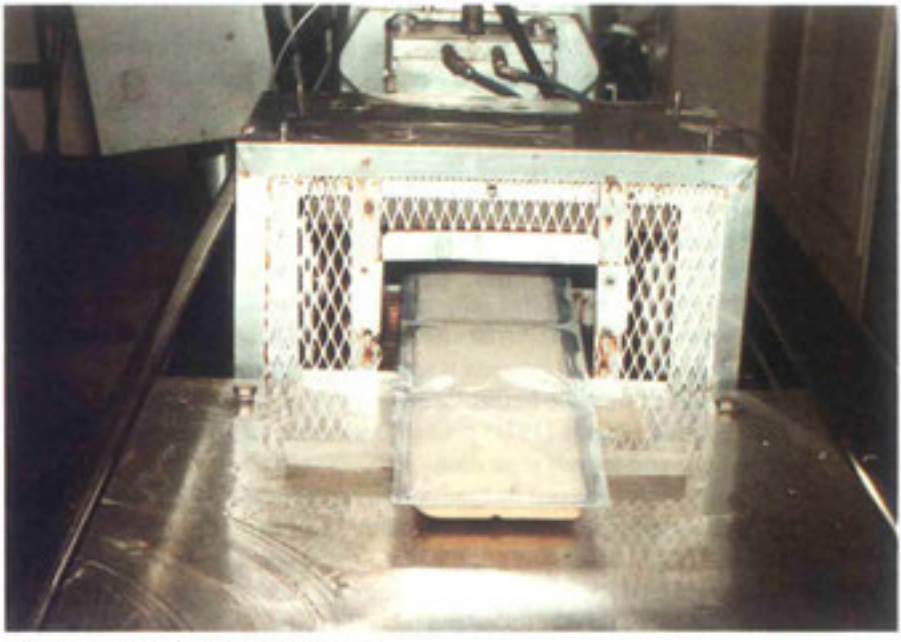

Figure 4. Boll weevil rearing trays.

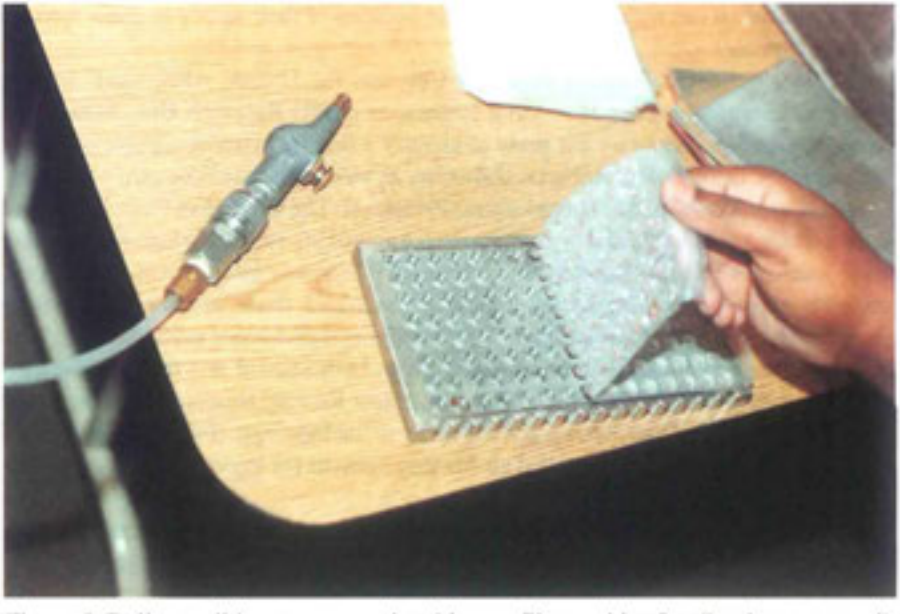

Figure 5. Boll weevil larvae encapsulated in parafilm cavities for *Catolaccus grandis* (Burks) parasite production.

TOBACCO BUDWORM AND BOLLWORM REARING

Tobacco budworm and bollworm propagation historically have presented challenges to insect rearing research. Most of the problems encountered have been focused on cannibalistic behavior and susceptibility to virus. Because of the difficulties that these problems have presented, earlier rearing procedures demanded that intense labor and extreme sanitation measures be incorporated into the operational procedures.

Early procedures involved inoculation of larvae into vials or cups to rear specimens individually (Berger, 1963). Burton and Cox (1966) modified a jelly-filling machine to mechanically fill cups with diet, and introduce eggs/larvae held in a corncob grit medium into the mechanically filled jelly cups. A tray method was developed by Roberson and Noble (1968) using Mylar Hexcel to inoculate eggs into 0.75 inch (1.9 cm) cells that were sandwiched between a sand base containing fungicide. A gelled diet slab was positioned over the hexcel sheeting, thereby encapsulating eggs within each cell. Raulston and Lingren (1972) published methods for large scale production using a light diffuser grid for cell separation.

The light diffuser tray developed by Raulston was modified by Hartley *et al.* (1982) by replacing cloth covers with an autoclavable plastic air filter for ease in preparation. Sparks and Harrell (1976) developed a mechanized tray production format for the bollworm. They adapted production to a flash sterilizer for diet preparation that pumped diet to a tray-forming unit for diet filling and larval inoculation. Studies also included development of pupal harvesting equipment. This mechanized system presented many advantages. However, problems were encountered when attempts were made to retain later stages of larvae within the rearing cells because of their ability to chew through strong materials.

In 1984, the Insect Rearing Research Unit and the USDA, ARS, Crop Science Research Laboratory, Corn Host Plant Resistance (HPR) Research Unit, Mississippi State, Mississippi, began a joint study to identify a lidding material capable of retaining larvae for the bollworm/tobacco budworm, as well as the southwestern corn borer, *Diatraea grandiosella* Dyar (Lepidoptera: Pyralidae). The Corn Host Plant Resistance Research Unit was interested in developing a tray rearing process adaptable to small-scale rearing, while the Insect Rearing Research Unit was interested in refining the methods proposed by Sparks to employ a combined flash sterilizer thermoform process. The joint study was successful in identifying a perforated mylar sheeting with hot-melt glue that could be used effectively with both manual and mechanized tray-assembly processes (Davis *et al.*, 1990). The Insect Rearing Research Unit then continued refinement of the mechanized process to include egg (Figure 6) and pupal (Figure 7) harvesting with improved air filtering systems for insect scales in the oviposition room (Roberson *et al.*, 1989).

Considering the difficulties encountered with disease and labor requirements, mass production of the tobacco budworm/bollworm complex in support of large-scale field release programs has been very successful. The tobacco budworm backcross experiment in St. Croix (U.S. Virgin Islands) demanded production of 10 million pupae during the period 1977-1980 (Proshold *et al.*, 1982). Operations were necessary to

Figure 6. Bollworm egg harvester.

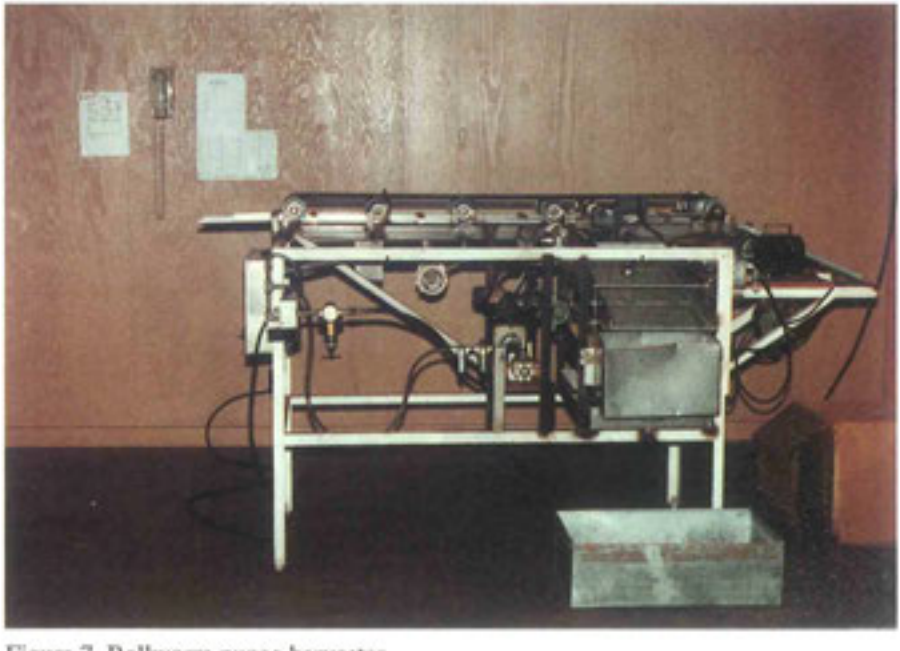

Figure 7. Bollworm pupae harvester.

produce, package and ship delicate pupae from the United States laboratories to St. Croix, then to effect placement in the field for emergence and flight from the release station. Field results indicate that the laboratory-reared insects successfully interacted with the feral (wild) moth population. Laboratory-reared females mated with wild males; males from their progeny were sterile and females transmitted the sterility trait to the next generation (see Chapter XVI, this book).

Review of rearing research programs illustrate the variable methods of production processes that are available for research projects. For the most part, propagation procedures used depend on the number of insects needed for a research project. Projects with extreme limitations of budget and space can purchase premixed diets or test specimens from commercial sources as needed.

Technologies developed in support of mass-rearing programs can produce rearing trays (Figure 8) capable of yielding 30,000 insects per operational hour. With advanced equipment, the production capacity could probably be 50,000 insects per operational hour. Additional advantages gained with the mechanized rearing procedure in which separate cells are formed for each insect reduce the stress of manual handling and shipping because pupae remain separated in self-formed pupation sites. Field emergence data of tobacco budworm backcross moths (Laster and Roberson, 1990) note significant pupal emergence rates from pupae emerging directly from trays (95 percent) vs. pupae removed from trays (56 percent).

As with boll weevil rearing technology, the status of mass-rearing technology for

Figure 8. Bollworm multiple cell rearing tray.

the tobacco budworm and bollworm is well advanced. The technology developed is adaptable to mass production for sterility control concepts, carcass production for pathogen production or host/prey supply for parasite and predator production. The historical problems relating to lack of specimen supply source due to unstable production for these insects should not impede progressive development of new biologically-based pest control concepts. The technologies developed are stable and, when properly administered, can be relied upon to support advanced research.

A manually oriented rearing process using reusable rearing trays is conducted within the USDA, ARS Southern Insect Management Laboratory at Stoneville, Mississippi. King and Hartley (1985) outlined methods for the tobacco budworm in which multicellular rearing trays were used to separate the cannibalistic larvae. This same technique was used for the bollworm and for the tobacco budworm sterile hybrid (Hartley *et al.*, 1982; King *et al.*, 1985). Yet another method for these pests uses dry diet flakes to separate larvae on trays of diet (Patana, 1985).

A few of the many earlier papers on bollworm/tobacco budworm rearing include: Barber (1936); Callahan (1962); Vanderzant *et al.* (1962); Berger (1963); Roberson and Noble (1968); Raulston and Lingren (1969); and, Young *et al.* (1976). Chauthani and Adkisson (1965) compared two artificial diets to determine effects on the biology of the bollworm or its response to insecticides. *Helicoverpa punctiger* (Wallengren), a serious pest of cotton in Australia, has been reared by Teakle and Jensen (1985).

As with the boll weevil, USDA-reared bollworms/tobacco budworms are made available for research purposes to public and private groups through a cooperative program with the Cotton Foundation.

PINK BOLLWORM REARING

The pink bollworm rearing and sterilization operations conducted by USDA's Animal and Plant Health Inspection Service in Phoenix, Arizona, stand as a model of advanced technology for stable insect rearing and sterilization. The program is scheduled to operate seven days per week and produce five million adults per day for a 150-day release period. To date, the program has been judged an effective tool for management of the pink bollworm, especially in keeping the pink bollworm from becoming a major cotton pest in the San Joaquin Valley in California. The USDA is currently conducting an extensive methods-development program to increase mechanization of the rearing operations. The rearing/sterilization operations and pink bollworm management programs are supported substantially by cotton producers in California.

Laboratory culturing studies were conducted at the USDA Pink Bollworm Research Laboratory, Brownsville, Texas. Larvae were inoculated in small vials with artificial medium and stoppered with cotton (Noble, 1969). The rearing procedures were modified by cubing the diet and layering hatched larvae/diet cubes/cotton in 9-ounce (265 ml) Dixie® cups to facilitate increased production needs (Noble, 1969). The inoculated cups were sealed with a plastic lid and layered in a standard 3-gallon egg collection container. As larvae developed to the last instar, they would chew through the paper

sidewall of the cups and pupate in shredded paper placed in the egg container bottom. Adults were collected by turning the lights off to cause flight of the emerged moths to a cone screen trap positioned on the lid of the container.

In 1966, the USDA, Methods Development section of APHIS, Plant Protection and Quarantine assumed rearing responsibilities to supply the sterile moths needed for release in the California San Joaquin Valley cooperative pink bollworm management program. In 1968, construction was initiated at the Phoenix, Arizona, production facility, with eventual expansion to rented warehouse space to facilitate increasing field demands for sterile pink bollworm moths. Serious difficulties in controlling microbial contaminants and viruses were encountered during the first years of expansion pressure. Technology was developed and implemented to improve egg treatment for cytoplasmic polyhedrosis virus (Stewart, 1984) and to develop mass-handling processes (i.e., larval cutout in hexcel, pupal collection and adult emergence). This enabled establishment and maintenance of large-scale, stable production.

Mass-rearing of the pink bollworm at the USDA facility in Phoenix, Arizona functions to supply competitive sterile moths in an effort to control this pest in California (Stewart, 1984). A discussion is provided on quality control and identified sources of contamination. In addition, a description of method and diet are given, along with information of quality control and life cycle data (Bartlett and Wolf, 1985).

PLANT BUG REARING

A proven method of rearing the western lygus bug, *Lygus hesperus* Knight, on artificial diet has been developed and used for many years (DeBolt and Patana, 1985). The method utilizes parafilm packets (Patana, 1982) of artificial diet (Debolt, 1982) for feeding and oviposition, and allows continuous rearing.

Oviposition in tissue paper has enhanced rearing methodology for the tarnished plant bug, *Lygus lineolaris* (Palisot de Beauvois) (Snodgrass and McWilliams, 1992). They found that plant bugs preferred to oviposit in moist tissue paper wrapped around a green bean rather than in a green bean. Traditionally, green beans have been used both as a food source and as an oviposition site in rearing. Disadvantages of oviposition in green beans include desiccation of beans, not knowing how many eggs have been laid, not being able to monitor development, and growth of mold or bacteria that can reduce egg hatch and survival of young nymphs. The new technique for extracting eggs and storing at a cold temperature for 15 days offers greater flexibility to rearing and research programs.

The tarnished plant bug has also been reared successfully on sprouting potatoes (Slaymaker and Tugwell, 1982) and lettuce (Stevenson and Roberts, 1973), but survival on artificial diet was poor (Vanderzant, 1967).

ARMYWORM REARING

Rearing methods for the beet armyworm, *Spodoptera exigua* (Hübner), have been described by Hartley (1990) and by Patana (1985). Hartley's (1990) method is similar to that used for tobacco budworm and bollworm rearing referred to earlier in this chap-

ter (Hartley *et al.*, 1982; King and Hartley, 1985; and King *et al.*, 1985). Rearing methods also have been reported for the Egyptian cotton leafworm, *Spodoptera littoralis* (Boisduval) (Navon, 1985), and for the Southern armyworm, *Spodoptera eridania* (Cramer) (Wright, 1985).

APHID REARING

Forbes *et al.* (1985) described rearing techniques for the green peach aphid, *Myzus persicae* (Sulzer) (Homoptera: Aphididae). Their methods can be applied to many species by changing the host plant and the timing. The cotton aphid, *Aphis gossypii* Glover, can become a serious pest of cotton, thereby necessitating a rearing program for testing.

QUALITY CONTROL STRATEGIES

Production quality control is used to monitor egg treatment, microbial contaminants, developmental rates, egg to adult yields, etc. The data collected provide critical insights to facilitate management to meet both quantity and quality of insects needed for use. Proper execution of established operational and sanitation procedures is the first step in maintaining production of high quality insects.

The importance of product quality control in insect mass production is recognized, as is evidenced by the attention given it in the literature. Chambers (1977), Chambers and Ashley (1984), Moore *et al.* (1985) and Leppla and Ashley (1989) represent only a small portion of the literature. In any progressive rearing program, changes are made continually in an effort to stabilize or improve production efficiency and insect quality. Unfortunately, many underfunded research programs can provide only minimal quality control support to rearing operations. As a result, marginal attention is given to sanitation, inbreeding or quality control standards for insect performance. Tabashnik and Slansky (1987) may give researchers insight into aspects of nutritional ecology that may enhance rearing of cotton insects. Maintenance of genetic diversity also contributes to improved insect quality; guidelines are discussed by Bartlett (1985).

RESPONSIBILITY FOR FIELD EVALUATION

Successful delivery and establishment in the field are essential for insect management effectiveness. Transportation and field dispersal of mass reared insects demand great attention to insure rapid release of healthy insects. Because of the intense operational demands of large insect release control tests and labor shortages for working closely with release operations, field dispersal of live organisms can be untimely and insect vitality decreased. Delays and mishandling during sterility treatments, packaging, transport, storage and field release may render an effective insect ineffective in the field.

To acquire the full benefit of a released insect, a strong effort must be directed to recognize and establish acceptable field release procedures. To release healthy insects, establishment and monitoring of handling procedures from the rearing facility to the

field is imperative. Handling operations involving extreme temperatures, extensive holding periods or harmful field release conditions can lower the vigor of shipped insects. These conditions can affect their ability to become established in the field and result in low survival of the insects during release operations.

Close communication between laboratory production and field release personnel is essential to synchronize insect development with desired time of release. Considering the financial investment of insect production and field release operations, a ground crew should be maintained to monitor field release conditions and to coordinate field dispersal personnel to improve the chance of successful establishment of field-released insects.

TECHNOLOGY TRANSFER

Most large scale rearing operations are developed by mechanizing small scale rearing procedures. Without mechanization, the quantity of insects required by massive field release programs could not be met. Major modifications from research to production therefore must be incorporated into the rearing methodology to meet production demands. This transition must be smooth, organized and timely, and current research systems organized for greatest efficiency. USDA research groups in the Agricultural Research Service and the Animal and Plant Health Inspection Service should be organized with compatible equipment and increased interaction of line personnel. This will maximize production and improve technology transfer. The Animal and Plant Health Inspection Service will benefit by gaining trained personnel and equipment to advance directly into mass production status. The Agricultural Research Service must continue to work closely with the Animal and Plant Health Inspection Service in directing full attention to deficient technology. Although few USDA insect rearing programs have interested commercial investors, their participation as suppliers or contractors for insects can fill pest control voids created by restrictions in pesticide use.

The need exists for a process to guide programs from research to development, with subsequent field testing and commercial employment. This will facilitate continuing progress and addressing new problems by rearing research groups. Although the organization to manage newly developed technologies is difficult, such a system is feasible. The requirements are that: (a) insect rearing technology be designed for cost effectiveness and adaptability to commercial application; (b) a legal protocol be established to advertise and to promote transfer of technology; and (c) actions be initiated to establish acceptable quality control and field evaluation standards. Further, government and industry must cooperate to establish an equitable system for identifying research needs, level of technology needed and a protocol for technology transfer.

SUMMARY

Many insects associated with cotton can be mass-reared using automated equipment. As this technology is developed, transfer to an action agency or to private industry is necessary for expanded use in applied operational programs. Research in insect rearing must be supported for production of high quality insects that are competitive and effective in the field. Insects must be reared for parasite development, production of pathogens, sterile release technology, hybrid sterility programs and other specialized uses.