Chapter 12

HORMONAL RELATIONS DURING REPRODUCTION

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INTRODUCTION

Plant growth substances have been implicated in the regulation of flower initiation, fruit abscission, and cutout. Many of the results are inconclusive, inconsistent or contradictory, especially in the case of flower initiation. Factors that regulate fruit retention or abscission are more firmly established. Publications on abscission are extremely numerous, but there is still some uncertainty about the roles of abscisic acid, gibberellins and cytokinins. Beyond the fact that an increasing percentage of fruit abscission is one aspect of cutout, very little has been published on the hormonal regulation of cutout. In this chapter I will attempt to review the current knowledge of flower initiation, fruit abscission, and cutout, and point out some areas that need additional research.

FLOWER INITIATION

Information on hormonal control of flower initiation in cotton is almost nonexistent. Most of the research has been done with flower initiation in photoperiodic plants, or plants that require vernalization to flower. Although ancestral cottons are short-day plants (Mauney and Phillips, 1963), most of the cultivated cottons are day-neutral and, therefore, could be classed as self-inductive. Perhaps because most cultivated cottons flower readily, few investigators have included cotton in their research on floral induction. Halevy (1972) did review the literature on the roles of phytohormones in the regulation of flowering of self-inductive plants, but he was concerned only with horticultural crops and did not mention cotton. He concluded that there is no reason to assume that the very complicated and variable process of flowering is regulated by a single, universal, and unique organ-forming hormone.

Mauney (1966) investigated the effects of day and night temperatures and photoperiod on flowering of a day-neutral cotton but did not investigate possible hormonal effects. Flowering was induced at a lower node by low night temperatures or by low day temperatures when the night temperature was 32C. Flowering

also occurred at lower nodes under 14-hr than 8-hr days, perhaps because of increased photosynthate supply. The promotive effect of low night temperatures also suggests an effect of carbohydrate availability because dark respiration would be greater at the higher temperatures. Hesketh and Hellmers (1973), however, found that increased CO_2 did not lower the position of the first fruiting branch, but raised it. They concluded that floral initiation is a bit more complex than can be explained on the basis of photosynthate supply.

Searle reviewed the physiology of flowering in 1965. At that time much effort had been given to proving the existence of a postulated flowering stimulus named "florigen." The production of florigen was presumed to be controlled by the balance between the red and the far-red absorbing forms of phytochrome. Because certain nucleic acid antimetabolites inhibited flowering, florigen was thought to act in gene activation or gene derepression. Chailakhyan (1968) suggested that florigen consists of two groups of hormonal substances: (a) gibberellins, which induce stem formation and growth, and (b) anthesins, which induce flower initiation. Neither anthesins nor florigens have ever been isolated or identified; evidence for their existence is based on experiments designed to show transmission of the flowering stimulus from induced to noninduced tissue. According to Chailakhyan (1968), gibberellins stimulate stem growth in both long-day and short-day plants, but stimulate flowering only in long-day species.

So many exceptions can be found that it is dangerous to generalize about the roles of phytohormones in flower induction. In the preface of a book on the induction of flowering that he edited, Evans (1969) commented, "Such diversity is only too apparent in the flowering processes of higher plants, to the frustration of reviewers and to the confusion of readers." Therefore, it is probably futile to use results obtained with other plants in an attempt to predict the effect of various hormones on flowering in cotton.

Zeevaart (1976) reviewed the physiology of flower formation and stated that all efforts to identify the floral stimulus have met with failure. He reviewed the effects of ethylene, cytokinins, gibberellins and abscisic acid (ABA). The effects of each of these hormones varied with different plants.

A few workers have investigated the effects of gibberellins (GA) on flowering in cotton. Dransfield (1961) found that five applications of 10 ppm GA, approximately 7 days apart, increased the number of flowering points, but higher concentrations decreased the number of flowering points, especially when applied early. The higher the concentration, the greater was the inhibition. A single application of 100 ppm GA decreased the number of flowering points. He concluded that GA application is of no practical benefit to cotton in northern Nigeria.

Jackson and Fadda (1962) obtained similar results. An application of 100 μg of GA per plant retarded flowering of young plants. Application of 100 and 500 μg of GA per plant 34 days after planting delayed flowering by 6 and 11 days, respectively. At 61 days after planting most of the differences had disappeared; the authors recorded averages of 6.7, 8.6, 6.9 and 1.7 squares per plant on plants

that had been treated with 0, 10, 100, and 500 μg of GA, respectively.

Ethylene may stimulate flowering of cotton. During two seasons Hall *et al.* (1957) observed a field of cotton that was near a polyethylene plant in Texas. Ethylene that escaped from the plant caused malformation of leaves, loss of apical dominance, and earlier and more profuse flowering than normal. Plants produced up to 400 squares each, but most of the squares abscised because ethylene was continually present as an air pollutant. The profuse squaring may have resulted, at least in part, from a lack of any boll load. In other tests, they noted that cotton plants did not produce a significant amount of ethylene until initiation of the reproductive stage. Evans (1969, p. 475) noted that, under non-inductive photoperiods, "Flowering in several short-day plants can be evoked by a temporary stress to growth—by drought, transplanting, nutrient stress, low temperatures, or the application of growth retardants or abscisin." It appears to be a rather common belief in irrigated areas that flowering of cotton can be induced or stimulated by withholding water early in the growing season. A preflowering stress has been observed to increase subsequent rates of blooming (Singh, 1975; Mauney *et al.*, 1980; Kittock, personal communication) and yield (Singh, 1975; El-Zik *et al.*, 1977). Water deficit increases ethylene production in petioles (McMichael *et al.*, 1972) and abscisic acid content of leaves (Milborrow, 1974). Although these results are suggestive, more research is needed to establish a causal role for ethylene and ABA in the induction of flowering in cotton.

Drought may sometimes increase early flowering through an effect on insects. Mauney *et al.* (1980) reported that early flowering was increased about 25 percent when the first post-emergence irrigation was delayed by two weeks. Plant bug populations were lower and square shedding was less in the plots in which irrigation was delayed. They also measured total fruiting positions and found that they were not increased by delaying the first irrigation (unpublished). They concluded that reduced insect damage was the major cause of the increased rate of early flowering in stressed plots.

FRUIT ABSCISSION

Once the cotton plant starts producing flower buds (squares) it usually continues doing so until cutout (see Chapter 2). In most cases a careful examination of plants that have "gone vegetative" will reveal that they have not reverted to producing monopodial (vegetative) branches. Rather, they are still producing sympodial (fruiting) branches, but a large percentage of the squares or young bolls are shedding. The internodes may be longer and the leaves larger than those of normally fruited plants, and the plants themselves may be taller. They appear vegetative because few squares and bolls are present at the fruiting sites. However, poor soil conditions and extremely high temperatures may cause some cultivars to actually revert to the production of monopodial branches in Pakistan (M.N.A. Malik, personal communication). I have never observed this kind of

reversion from sympodial to monopodial branch production in field-grown cotton in Phoenix even at temperatures up to 47C (117F). Excessive shedding of squares and bolls is the most likely situation in plants that have "gone vegetative."

ENZYMES INVOLVED IN ABSCISSION

Most of the research on the biochemistry and anatomy of abscission has been conducted with explants (small sections of stem plus petiole tissue with leaf or cotyledon blades removed).

Enzymic dissolution of the middle lamella and portions of the primary wall of cells in the abscission zone usually precedes abscission (Webster, 1973). Insoluble pectates, mainly calcium pectate, in the middle lamella are hydrolyzed to pectic acid. Increased pectinase activity usually precedes abscission (Yager, 1960; Zaitlin and Coltrin, 1964; Morré, 1968; Riov, 1974) but pectin esterase apparently has little or no effect (Ratner *et al.*, 1969; Moline *et al.*, 1972). Although pectinase activity may be sufficient to cause abscission (Morre, 1968), cellulase activity in the abscission zone also increases prior to abscission in most plants (Abeles, 1969; Ratner *et al.*, 1969; Lewis and Varner, 1970). These two enzymes, pectinase and cellulase, digest the middle lamella and soften portions of cell walls of cells in the abscission zone, thereby greatly weakening the petiole or peduncle at that point (Morré, 1968; Webster, 1973). Separation may not occur immediately even after break strength declines to a minimum (Morré, 1968), probably because of vascular tissue that has to be broken by mechanical forces. Enlargement of cells on the proximal side (the stem side of the abscission zone) and shrinkage of cells on the distal side (the leaf or fruit side) cause shear and tension forces that eventually break the vascular connections (Morré, 1968; Leopold, 1971; Osborne, 1973). This may explain the observation that abscission does not normally occur during the period of drought stress and that separation does occur after plants are rewatered (Osborne, 1974). Increased turgor and resultant swelling of proximal cells could increase the tensile forces on vascular elements through the abscission zone and cause them to break.

Evidence indicates that pectinase and cellulase are synthesized *de novo* before abscission (Abeles, 1968; Ratner *et al.*, 1969; Lewis and Varner, 1970; Abeles *et al.*, 1971; Riov, 1974) and that the cellulase is different from cellulase already present in cells (Lewis and Varner, 1970; Reid *et al.*, 1971; 1974). Because the sites of action of pectinase and cellulase are the middle lamella and the primary cell wall, and the site of synthesis of these enzymes is within the plasmalemma, they must be secreted before they can cause abscission (Morré, 1968; Abeles and Leather, 1971; Abeles *et al.*, 1971b; Gilliland *et al.*, 1976; Addicott and Wiatr, 1977). If pectinase and cellulase are required to dissolve the middle lamella and weaken the primary cell wall of cells in the abscission zone, as appears to be the case, then an explanation of inhibition or promotion of abscission by environmental and hormonal factors must eventually tie these factors to regulation of synthesis, secretion and activity of these hydrolytic enzymes.

HORMONAL EFFECTS

Plant hormones apparently interact to control abscission. Auxin generally inhibits abscission (but there are exceptions); ethylene promotes abscission; and ABA, cytokinins and gibberellins have variable effects, depending upon concentration, site of application and tissue involved. In the following discussion, the hormones will be considered separately insofar as possible. However, because of interactions, it will be necessary to mention more than one hormone under each heading.

Auxins—It has been known for many years that auxins such as indole-3-acetic acid (IAA) and naphthalene acetic acid (NAA) inhibit abscission when applied to petiolar stumps of explants (Addicott and Lynch, 1955). However, when applied to the stem portion of the explant (proximal side of the abscission zone), IAA stimulated, rather than inhibited, abscission. This response caused Addicott and co-workers to propose the auxin-gradient theory of abscission control (Addicott *et al.*, 1955). According to this theory, the relative concentrations of auxin on each side of the abscission zone (the auxin gradient) are more important than the absolute auxin concentration. Rubinstein and Leopold (1963) found that time of auxin application was just as important as concentration. When they applied NAA immediately after deblading, the NAA inhibited abscission; if they waited 6 hours or longer, however, NAA then promoted abscission. Chatterjee and Leopold (1963) extended these results to IAA and the synthetic growth regulators, 2, 4-dichlorophenoxyacetic acid (2, 4-D), 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) and others. These data provided the basis for the "two-stage" theory of auxin action. (For a discussion of the auxin-gradient, the two-stage, and other theories to that time, see review by Carns, 1966).

The discoveries by Morgan and Hall (1962, 1964) that 2,4-D and IAA stimulate ethylene production in plant tissue provided a basis for explaining the observations that abscission is regulated by the auxin gradient and that auxins can either inhibit or promote abscission, depending upon site and time of application. Abeles (1967) explained the auxin-gradient effect on the basis of auxin stimulation of ethylene production, the polar movement of auxin, and the opposing effects of auxin and ethylene in inhibiting and promoting abscission, respectively. When applied distally, auxin moves into the abscission zone and inhibits abscission. When applied proximally, however, auxin is unable to move rapidly into the abscission zone (against its normal direction of polar movement). Ethylene can move in any direction and its promotive effect becomes dominant when auxin is applied to the proximal side of the abscission zone. The time-dependent effect of auxin in either inhibiting or promoting abscission was reviewed and explained by Leopold (1971). During stage I, the period during which auxin inhibits abscission, the tissue is relatively insensitive to ethylene. After deblading or excision, the tissue soon becomes sensitive to ethylene. During this stage II, auxin no longer inhibits abscission but may promote it because the applied auxin stimulates

ethylene production, and the tissue is now sensitive to the abscission-promoting effects of ethylene. Auxin tends to prolong stage I when applied soon enough.

Despite the vast amount of research that has been done on auxin, the exact mechanism by which it inhibits abscission has not been elucidated. Treatment with auxin prevented the increase in the specific cellulase that apparently causes abscission (Abeles, 1969; Ratner *et al.*, 1969; Lewis and Varner, 1970), but it is not clear whether the effect was due to a direct inhibition of synthesis of abscission-promoting cellulase or to an indirect effect (e.g., prevention of changes that result in senescence). The fact that the increase in cellulase activity was also suppressed by application of cycloheximide (Abeles, 1969; Ratner *et al.*, 1969) indicates that the increased cellulase activity was due to synthesis of new enzyme rather than to activation of pre-existing enzyme. Although speculative, another mechanism by which auxin might inhibit abscission is through an effect on membranes. Auxin has been reported to maintain membrane integrity and selective permeability (Sacher, 1957; Abeles, 1968; Helgerson *et al.*, 1976) and, therefore, may tend to prevent secretion of pectinase and cellulase through the plasma membrane. There is no direct experimental evidence to support such an hypothesis, however.

Ethylene—Although its role as a natural regulator of abscission was questioned in in the 1950's, ethylene is now firmly established as a potent abscission-promoting hormone. Two mechanisms of action have been established: (a) slower transport and increased destruction of auxin, and (b) stimulation of synthesis of pectinase and cellulase in the abscission zone.

Morgan and Hall (1962), Hall and Morgan (1964), and Morgan *et al.* (1968) showed that ethylene stimulates IAA-oxidase activity and decarboxylation of IAA in cotton. Morgan and co-workers also showed that ethylene slows auxin transport (Morgan and Gausman, 1966; Morgan *et al.*, 1968; Beyer and Morgan, 1969, 1970, 1971) and that inhibition of auxin transport promotes abscission (Morgan and Durham, 1975). Because auxin prevents or delays abscission, both the destruction and the slowed transport of auxin should promote abscission by decreasing the amount of auxin that reaches the abscission zone.

Perhaps an even more direct action of ethylene is its stimulation of synthesis of pectinase (Riov, 1974) and cellulase (Horton and Osborne, 1967; Abeles, 1968, 1969; Ratner *et al.*, 1969; Reid *et al.*, 1971) in the abscission zone. Not only does ethylene stimulate the synthesis of cellulase, it also promotes the release or secretion of cellulase through the plasma membrane and into the cell wall (Abeles and Leather, 1971; Abeles *et al.*, 1971). Without such secretion the enzyme could not, of course, digest the cell wall.

Thus, ethylene promotes abscission in at least two ways. It decreases the auxin content of the abscission zone, and it stimulates the synthesis of enzymes that weaken the middle lamella and cell wall.

Abscisic Acid (ABA)—The actions of ABA and ethylene are similar in many respects. ABA slows growth (Rehm and Cline, 1973), hastens senescence (De la Fuente and Leopold, 1968), decreases basipetal (toward the base) movement of IAA (Chang and Jacobs, 1973), promotes ethylene production and an increase in cellulase activity (Craker and Abeles, 1969; Jackson and Osborne, 1972), and may cause abscission (Craker and Abeles, 1969; Davis and Addicott, 1972; Cooper and Horanic, 1973; Varma, 1976). These similarities caused Addicott (1970) to suggest that ABA might function as a "non-volatile ethylene" in abscission.

Even though ABA was isolated and purified on the basis of its ability to stimulate abscission, its importance as a natural regulator of abscission has been questioned. Milborrow (1974b) reviewed the evidence to 1974 and concluded that ABA is not closely involved in the regulation of leaf abscission but probably does regulate fruit abscission. More recent evidence has cast doubt on its role as a direct regulator of fruit abscission. The situation is complicated by the fact that ABA can stimulate ethylene production in at least some tissues (Craker and Abeles, 1969; Abeles *et al.*, 1971; Jackson and Osborne, 1972; Sagee *et al.*, 1980). Therefore, its effects could be indirect (through increased ethylene) rather than direct. Some evidence suggests that ABA does have direct effects that are not dependent upon increased ethylene production. Craker and Abeles (1969) reported that ABA increased cellulase activity in both bean (*Phaseolus vulgaris* L.) and cotton explants above that caused by a saturating level of 10 ppm ethylene. Further, they found that ABA caused cellulase activity to appear about 4 hours sooner than with ethylene alone in bean, but not in cotton, explants. Cooper and Horanic (1973) used low pressures to remove ethylene from treated citrus. Hypobaric pressures prevented the fruit drop that normally occurs after spraying the fruit with cycloheximide, thereby implicating ethylene in the abscission induced by cycloheximide. However, hypobaric pressures did not prevent fruit drop after treatment with ABA, indicating that ABA did not depend upon ethylene to cause abscission. However, results obtained by Sagee *et al.* (1980) with citrus (*Citrus sinensis* L. Osbeck) leaf explants provided convincing evidence that ABA promoted abscission by stimulating ethylene production in that tissue. The addition of aminoethoxyvinyl glycine (AVG), an inhibitor of ethylene biosynthesis, prevented the increase in cellulase and polygalacturonase activity, and prevented a stimulation of abscission by ABA. AVG did not prevent an increase in the activity of these enzymes or of abscission when ethylene was supplied, thus indicating that the inhibition by AVG was specifically due to its effect in preventing ethylene biosynthesis. ABA stimulated ethylene production, cellulase and polygalacturonase activity, and abscission only in the absence of AVG.

The role of ABA in cotton boll abscission remains controversial. Dale and Milford (1964) and Cognée (1975) questioned the effectiveness of ABA in causing boll shedding because application of boll extract (Dale and Milford) or ABA (Cogneé) did not stimulate abscission in their tests. Application of 2 or 10 μg of

ABA to the calyx cup the day after anthesis caused no change in abscission rate (Cognée, 1975). Addition of 6.6 μg of ABA to the calyx cup stimulated abscission only when plants were stressed by a water deficit (Guinn, unpublished). In contrast, Varma (1976a) reported a stimulation of abscission by much less ABA, 0.66 and 0.13 μg per boll. Because ultraviolet light causes a rapid destruction of ABA (Johnson and Ferrell, 1982), it may be broken down before it is absorbed. To decrease this possibility, Guinn (unpublished) injected 25 μl of 1 mM ABA directly into 3- and 4-day-old bolls. Injection of ABA caused no more abscission than the solvent alone (4% methanol in water). Most of the evidence for a role of ABA in stimulating boll abscission is either circumstantial or was obtained with explants.

Gibberellins—Gibberellins have been reported to increase abscission (Carns *et al.*, 1961; Valdovinos and Ernest, 1967; Wittenbach and Bukovac, 1973; Morgan and Durham, 1975; Varma, 1976; Chatterjee, 1977) and conversely, to decrease abscission (Walhood, 1957; Carns *et al.*, 1961; Bhardwaj and Dua, 1972; Bhardwaj *et al.*, 1975; Varma, 1976). In general, GA appears to promote abscission of explants, except at low concentration applied proximally to the abscission zone (Carns *et al.*, 1961), and to retard abscission of intact fruits (review by Addicott, 1970; Varma, 1976). These apparently conflicting effects probably result from indirect effects of GA, some of which may promote, and others retard, abscission. Gibberellins may retard abscission of intact fruit by mobilizing nutrients to that fruit and by stimulating growth (Addicott, 1970). When Walhood (1957) applied GA directly to some cotton fruits, the treated fruits did not abscise, but untreated fruits on the same plant showed increased abscission. When Johnson and Addicott (1967) treated all fruits on a plant with GA, the treatment did not increase retention. These results suggest an increase in the competitive ability of GA-treated cotton fruits. Such a mechanism could not operate in explants, and other effects of GA might then stimulate abscission. Two such effects are the stimulation of ethylene production by GA observed by a few workers (cf. review by Abeles, 1973) and the enhancement of ethylene action (Morgan and Durham, 1975). Another consideration is the fact that there are many gibberellins and they may not all have the same effects.

Most results suggest, however, that GA retards abscission of young cotton bolls. Walhood (1957) was able to increase boll set by treating with GA. Bhardwaj and Dua (1972) found unusually low concentrations of auxins and gibberellins in seeds of 'H 14', a high-shedding cultivar. Application of GA_3 alone or with IAA or IAA and kinetin even caused retention of bolls that developed from emasculated flowers (Bhardwaj *et al.*, 1975). Although GA promoted abscission of buds and boll explants, it retarded the shedding of intact bolls and counteracted the abscission-promoting effect of applied ABA. According to Varma (1976a), GA was more effective than naphthalene acetic acid (NAA) in counteracting the effect of ABA. In contrast, Cognée (1975) found that NAA was completely ineffective in preventing boll abscission; only gibberellin or mixtures containing

gibberellin were effective. Gibberellin content remained low in bolls destined to abscise and increased in retained bolls (Cognée, 1975). Rodgers (1981c) reported maximum gibberellin activity at about 2 and 15 days after anthesis, ages at which he found relatively little boll abscission (Rodgers, 1980a).

Cytokinins—The role of cytokinins in regulating abscission appears to be indirect. They may either inhibit or promote abscission, depending upon time and site of application (cf. review by Addicott, 1970). Cytokinins delay or prevent senescence and promote the ability of an organ to compete for metabolites (Letham, 1967). These effects are probably related because the ability to accumulate the metabolites necessary for growth would tend to prevent senescence. Because senescence increases the sensitivity of an organ to the abscission-promoting effects of ethylene (De la Fuente and Leopold, 1968; Leopold, 1971), any hormone that prevents senescence should also prevent or retard abscission. Bhardwaj *et al.* (1975) suggested that seeds promote boll retention through their production of auxins, gibberellins and cytokinins.

Exogenous applications of cytokinins can promote, rather than retard, abscission. Varma (1976a) reported that cytokinin treatments promoted boll abscission except those applied directly to the abscission zone, which decreased boll shedding. These results agreed with earlier results obtained with explants of bean by Osborne and Moss (1963) who interpreted these results as indicating that mobilization of nutrients away from the abscission zone would cause senescence there and lead to abscission.

Rodgers (1981b) measured cytokinin activity in retained and abscised bolls. Retained bolls contained slightly higher concentrations of cytokinin activity at 7 and 10 days after anthesis than abscised bolls. Retained bolls contained much more cytokinin per boll because they were much larger than abscised bolls. He postulated that, because cytokinins are involved in mobilization of metabolites, weak fruits do not have as much capacity for cytokinin synthesis or accumulation as strong fruits. Therefore, they are not able to compete as well for nutrients and do not grow as much as strong fruits. Slow growth is typical of bolls that are destined to abscise (Cognée, 1975; Rodgers, 1980a).

OTHER SUBSTANCES

Senescence usually precedes abscission (Abeles *et al.*, 1968; Burg, 1968; Leopold, 1971). An increase in ethylene production accompanies senescence, but it is not clear which is cause and which is effect. Apparently, an increase in ethylene production can both cause (Burg, 1968; Abeles *et al.*, 1971b; Chatterjee and Chatterjee, 1972; Mayak *et al.*, 1977) and result from (Hulme *et al.*, 1968; Osborne *et al.*, 1972; Beutelmann and Kende, 1976) aging and senescence. A loss of membrane integrity coincides with senescence (Osborne *et al.*, 1972; Ferguson and Simon, 1973; Beutelmann and Kende, 1976). Osborne *et al.* (1972) obtained evidence that the loss of membrane integrity stimulated ethylene evolution and abscission. They obtained a material from aqueous diffusates from senescent

petioles and leaf blades that stimulated ethylene evolution by, and abscission of, explants. This substance, which they called senescence factor (SF), was acidic and nonvolatile, but did not have the chromatographic properties of ABA. This SF leaked from senescent tissue and could be extracted from green healthy tissue with ethanol. They postulated that SF is of general occurrence in plants and that it functions as a regulator of ethylene production. They also postulated that SF is normally kept separate from the site of ethylene biosynthesis by membrane compartmentation, but that wounding or senescence could modify membrane permeability and permit SF to diffuse to the site of ethylene biosynthesis. This concept, if shown to be valid, would provide an explanation for many environmental causes of abscission. Any condition which increases membrane permeability or causes loss of membrane integrity would stimulate ethylene production and abscission.

A few other workers have attempted to determine the properties of an endogenous senescence factor. Chang and Jacobs (1973) extracted a SF from *Coleus blumei* Benth, and reported that it decreased the basipetal movement of IAA in explant petioles. It also accelerated abscission. The effects and properties of their SF were similar to those of ABA. Prakash (1976) attached senescent and nonsenescent petioles and leaves of *Catharanthus roseus* [(L.) G. Don] to explants. The senescent tissue promoted abscission of the explants, but nonsenescent petioles and, especially, nonsenescent leaves retarded abscission. However, membrane compartmentation of SF in nonsenescent tissue would have prevented movement of SF into the explant. Diffusion of auxin from the healthy tissue may have retarded abscission. Guinn (1977) extracted a heat-stable material from cotton bolls, after destroying membranes by freezing, which stimulated ethylene evolution in healthy bolls. Injection of various organic solvents into young cotton bolls increased leakiness of membranes (as indicated by discoloration, a water-soaked appearance, and increased electrical conductivity) and greatly stimulated ethylene evolution. The stimulation of ethylene evolution was generally proportional to membrane damage (Guinn, 1977).

In the absence of isolation, purification and chemical identification, it is impossible to know whether the senescence factors investigated by various workers are indeed the same substance. The acidic, nonvolatile SF of Osborne *et al.* (1972) and the heat-stable stimulator of ethylene biosynthesis extracted from bolls (Guinn, 1977) may have been 1-aminocyclopropane-1-carboxylic acid (ACC). Adams and Yang (1979) and Lürssen *et al.* (1979) obtained evidence that ACC is an immediate precursor of ethylene.

Various amino acids have been reported to stimulate abscission; these include alanine, glutamic acid, serine, glycine, aspartic acid, phenylalanine, methionine, glutamine and histidine (Rubinstein and Leopold, 1962; Chatterjee, 1977). At least two possible explanations can be given for the stimulation of abscission by amino acids. First, certain amino acids such as serine, cysteine, glycine and alanine promote senescence, presumably by stimulating the synthesis of proteases

(Martin and Thimann, 1972). Secondly, methionine is the precursor of ethylene in higher plants (Lieberman and Mapson, 1964; Lieberman *et al.*, 1966; Baur *et al.*, 1971; Owens *et al.*, 1971). A third possible reason suggested by Addicott (1969, 1970) implicates the amino acids in the synthesis of hydrolytic enzymes, such as cellulase, in the abscission zone. Addicott also suggested that amino acids could contribute methyl groups for the methylation of calcium pectate and thus render the pectins in the middle lamella more soluble. However, Rubinstein and Leopold (1962) found a poor correlation between methyl donor activity and stimulation of abscission.

Ascorbic acid has been investigated by a few workers, but the results appear inconsistent (cf. review of Addicott, 1970). Varma (1976a) reported that ascorbic acid decreased cotton boll abscission and counteracted the promotive effects of ABA. The inhibitory effects of ascorbic acid might be due to its antioxidant activity. Auxin can be destroyed by IAA oxidase activity. Further, the production of ethylene requires oxygen (Baur *et al.*, 1971), but, to my knowledge, it has not been shown that ascorbic acid inhibits ethylene production.

As we have seen, many substances can affect abscission, but few directly control the synthesis, secretion and activity of pectinase and cellulase in the abscission zone. Auxin, ethylene and ABA appear to be the hormones most directly involved. Other hormones and substances can affect abscission indirectly through their effects on growth, mobilization of metabolites, auxin synthesis, auxin transport, senescence and promotion of synthesis of ethylene and, possibly, ABA. The control of abscission does not reside in any one hormone, other substance, or environmental factor, but is regulated by the complex interaction of hormones, nutrients and the environment.

CUTOUT

Strictly speaking, cotton is an indeterminate plant because it flowers and sets fruit over an extended period. However, breeders have developed cultivars that fruit early and stop growing and flowering sometime during the season. We refer to such cultivars as determinate even though, botanically speaking, they too are indeterminate. The differences between "determinate" and "indeterminate" cottons are not absolute, but cover the entire range from the most to the least indeterminate. The differences between "determinate" and "indeterminate" cottons are not absolute but cover the entire range from the most to the least at a lower node (Ray, 1972), shed fewer early squares, and require fewer days between fruiting positions on each branch and between successive branches (Namken *et al.*, 1975). As the boll load increases, fruit abscission rates increase and rates of growth and blooming slow and may eventually stop (Eaton, 1955; Ehlig and LeMert, 1973; Verhalen *et al.*, 1975; Patterson *et al.*, 1978). This hiatus in growth and fruiting is commonly referred to as "cutout". If the season is sufficiently long, growth and fruiting resume after some of the bolls open. Inde-

terminate cultivars set fruit at a more leisurely pace, and the boll load may never be heavy enough to cause the plants to cut out. Although the existence of cutout has been recognized for many years, its causes are not completely understood.

Soil, insect and climatic factors affect the genetic expression of determinacy and cutout (see Chapters 4 and 7). Ewing (1918) noted that, "It is a matter of common observation that the cotton plant will generally fruit much more rapidly and that the crop will mature earlier on sandy or loam soils than on clay soils, or on well-drained than on poorly drained land." Adequate soil moisture delays cutout; whereas, drought hastens it (Crowther, 1934a; McNamara *et al.*, 1940; Hearn, 1975). Nitrogen deficiency causes early cutout, whereas adequate nitrogen prolongs growth and fruiting (Tucker and Tucker, 1968; Hearn, 1975; see also Chapter 10).

Insects can delay cutout by decreasing the rate at which plants set bolls. Removal of squares or blooms stimulates subsequent fruiting and delays cutout. Eaton (1955) reviewed several experiments that showed stimulation of subsequent fruiting after early squares or blooms were removed. Ehlig and LeMert (1973) removed no flowers from the control plots and removed all flowers from treated plots until June 26, July 15, July 30 or August 14. Flower removal delayed boll shedding and cutout in proportion to the delay in boll loading. They concluded that fruit load, rather than high temperature or humidity, was the primary cause of low boll retention and cutout. Patterson *et al.* (1978) compared partial defruiting treatments in which they left all flowers on the plants (control) or left one flower per plant every 2, 3, 4 or 5 days. Defloration increased the number of blooms produced, decreased boll abscission and delayed cutout in proportion to the number of blooms removed. Deltapine Smooth Leaf (a relatively determinate cultivar) responded more than Acala 44-10 (a less determinate cultivar). They concluded that boll load exerts a large influence on fruiting behavior and is the major controlling factor of cutout (see Chapter 6).

Developing bolls are strong sinks for carbohydrates and nitrogen, and this competition is apparently a factor in cutout. Sink strength increases with boll age and reaches a maximum about 20 to 30 days after anthesis (Pinkhasov and Tkachenko, 1981). Bolls that were 27 days old incorporated far more radioactivity from ^{14}C-labelled leaves near the tops of plants than did 7- and 10-day-old bolls, even though the younger bolls were much closer to the source leaves. Counting from the base, mainstem source leaves were at nodes 10, 11 and 12. The bolls were at the first sympodial node of branches at mainstem nodes 5, 9 and 10 for bolls that were 27, 10 and 7 days old, respectively. The older bolls, therefore, were able to attract photosynthate from leaves that were at least 5 mainstem nodes away. Because older bolls are such powerful sinks their presence probably deprives growing points, younger bolls and roots of needed sugars.

A higher rate of photosynthesis should delay cutout by providing more sugars. Mauney *et al.* (1978) reported that enrichment of the atmosphere with CO_2 increased the rate of photosynthesis and delayed cutout by about 10 days. Plants

in high CO_2 produced twice as many bolls as plants in normal CO_2 before they cut out. Earlier work (Guinn *et al.*, 1976) had shown that plants in high CO_2 used more nitrate than those in normal air, and the full benefits of high CO_2 were obtained only when the supply of inorganic nutrients was doubled.

A heavy boll load might induce a nitrogen deficiency by competing for nitrogen and by restricting root growth and activity through competition for sugars. Bolls appear to be stronger sinks than roots because the presence of developing bolls greatly restricts root growth; defruiting caused almost a 3-fold increase in root weight (Eaton, 1931; Eaton and Joham, 1944). Crowther (1934a) postulated that bolls so dominated the plant that roots stopped growing and absorbing nitrogen. Thus, according to Crowther, nitrogen uptake is interrupted just when the demand is greatest. The limitation on root growth might also decrease the uptake of other nutrients and water. Thus, direct competition by developing bolls for sugars and nitrogen and indirect effects on nutrient and water uptake by roots would probably restrict the growth of shoot meristems.

Hormones have functions that should affect growth, fruiting and cutout. Auxin increases cell wall plasticity and water uptake, and these effects are probably major factors in stimulation of cell elongation by auxin (Galston and Purves, 1960). Auxin also enhances the synthesis of RNA and protein (Sacher, 1969), maintains differential permeability of membranes (Galston and Purves, 1960), increases assimilate mobilization (Patrick and Wareing, 1976), and delays senescence (Sacher, 1969). The role of auxin in suppressing abscission was discussed earlier.

Cytokinins are the most effective senescence retardants known (Letham, 1967). They promote the synthesis of RNA, protein and lipid; inhibit nuclease and protease activities; promote the transport, accumulation and retention of metabolites; promote cell division and enlargement; and delay senescence (Osborne, 1962; Letham, 1967; Skoog and Armstrong, 1970). The retardation of senescence appears more directly related to the role of cytokinins in maintaining nucleic acid and protein levels than to mobilization of metabolites (Osborne, 1962; Adedipe and Fletcher, 1971).

Gibberellins stimulate IAA production in some plants (Anderson and Muir, 1969; Jones, 1973) and this complicates the interpretation of their action. They also cause an increase in phospholipid synthesis (Koehler and Varner, 1971, 1973) that may relate to maintenance of selective permeability of membranes (Jones, 1973). Gibberellins promote substrate mobilization, cell elongation and division, and growth of dormant buds (Jones, 1973). Walhood (1957) reported that application of gibberellins to the apical buds of cotton plants in all stages of cutout was followed by an immediate resumption of growth.

Abscisic acid counteracts many of the actions of auxins, cytokinins and gibberellins. ABA inhibits the synthesis of protein, RNA and DNA; inhibits growth; and prolongs bud dormancy (Addicott and Lyon, 1969; Rehm and Cline, 1973; Milborrow, 1974). It also causes stomatal closure (Milborrow, 1974b) and, thus, should inhibit photosynthesis.

As mentioned earlier, ethylene increases abscission and, thus, probably is a factor in the increasing rate of boll abscission that occurs with increasing boll load. Ethylene also inhibits cell elongation and growth (Abeles, 1973). However, unlike ABA which prolongs bud dormancy, ethylene apparently breaks bud dormancy. Hall *et al.* (1957) reported that high concentrations of ethylene caused loss of apical dominance.

Environment and boll load probably cause hormonal changes that affect cutout. According to Ewing (1918), Balls ascribed the cessation of growth and flowering to self-poisoning. Eaton (1955) stated that, "A demonstration of the existence and mode of action of a mobile growth regulating material (anti-auxin) from developing cotton bolls would go far toward explaining some of the growth behaviors of the cotton plant." The isolation of abscisin from cotton bolls established the existence of such a material, because it was shown to have anti-auxin activity (Carns *et al.*, 1955). If ABA produced in bolls is translocated, or if boll load causes the production of ABA elsewhere in the plant, ABA could be an important hormone in causing cutout. Creelman and Sabbe (1976) reported that foliar application of ABA decreased terminal growth. They also stated, on the basis of Creelman's dissertation (Creelman, 1975), that boll-produced ABA is translocated to fruiting branch terminals. They postulated that the ABA activity could reduce the rate of elongation of the fruiting branch, reduce the production of fruiting sites, and be a factor in cutout.

Limitation of root growth, because of competition by developing bolls, could also affect hormonal balance. Evidence obtained with a number of plants indicates that roots produce cytokinins and, probably, gibberellins for transport to the shoot (Torrey, 1976). Roots may also affect IAA content of shoots. Guinn (unpublished) found measurable amounts of tryptophan, a precursor of IAA, in xylem sap but not in leaves of cotton. If restricted root growth results in a water deficit, ABA content of shoots may be increased, and cytokinin content may be decreased (Vaadia, 1976). A nitrogen deficit might also decrease the cytokinin and IAA content of shoots because these hormones contain nitrogen. Sattelmacher and Marschner (1978) reported that nitrogen deficiency decreased the cytokinin activity in root exudate and shoots of potato (*Solanum tuberosum* L.) plants. Conversely, a nitrogen deficit might increase ABA content of shoots. Mizrahi and Richmond (1972) reported an increase in ABA content of tobacco (*Nicotiana rustica* L.) leaves after they transferred the plants from nutrient solution to distilled water. Goldbach *et al.* (1975) showed that a nitrogen deficiency increased the ABA content of sunflower (*Helianthus annuus* L.) leaves; and Radin and Ackerson (1981) showed the same thing for cotton leaves.

From the preceding examples, we can see that there are probably complex interactions between hormones and competition for organic and inorganic nutrients. Hormonal balance can both affect and be affected by competition for organic and inorganic nutrients. Auxins, cytokinins, and gibberellins promote

growth, whereas ABA and ethylene inhibit growth, and ABA promotes bud dormancy. Ethylene also stimulates boll and, possibly, square abscission. The balance between the growth-promoting hormones on the one hand and ABA and ethylene on the other probably mediates growth, fruiting, abscission and cutout in cotton.

SEQUENTIAL CHANGES AND INTERACTIONS

Work with other plants indicates that auxin production increases after pollination and that young developing embryos are a source of IAA (Addicott and Lynch, 1955; Crane, 1964). Dale and Milford (1964) extracted a growth promoter from cotton bolls of various ages that may have been IAA; it had Rf values similar to those for IAA in the eight solvent systems used. Their promoter was present in relatively small amounts for the first 5 days after anthesis. It then increased slightly to a small peak on day 8, declined somewhat the following 2 days, and then increased gradually to a second and higher peak 26 days after anthesis. Rodgers (1981a) estimated the auxin content of bolls (by bioassay) from anthesis until the bolls were 50 days old. He found peaks of activity at 3 and 15 days, and a smaller peak at 30 days, after anthesis (Figure 1). Auxin content of lint plus seed followed a similar pattern except that the concentration was higher. His results do not agree very well with those of Dale and Milford (1964), possibly because of differences in cultivar and environment.

Davis and Addicott (1972) determined the ABA content of two Acala cultivars as influenced by boll age and time during the season. The ABA content increased with boll age to a maximum at 10 days after anthesis, declined to a very low level at 20 days, remained at a low level until 30 days, and then increased to a second maximum at 50 days after anthesis. Rodgers (1980b) obtained similar results, although he found the highest concentration of ABA-like material on the day of anthesis. This declined to a minimum at day 3 and then increased to a second, but lower, maximum 7 days after anthesis (Figure 2) rather than at 10 days as reported by Davis and Addicott (1972). Fruit walls contained much higher concentration of ABA than lint plus seed except at 40 days after anthesis (Davis and Addicott, 1972; Rodgers, 1980).

Lipe and Morgan (1972a, 1973b) determined the rate of ethylene production in bolls of different ages. They reported (Lipe and Morgan, 1972a) that ethylene production reached a maximum on the day of anthesis and then declined to low values 4 days later. In a later paper (Lipe and Morgan, 1973b), they reported that ethylene production increased in bolls "during a period of considerable fruit abscission." Maximum rates of ethylene production either preceded or coincided with boll abscission. They noted a daily fluctuation in rate of ethylene production with the minimum rate occurring at night.

Guinn (1976a) and Guinn *et al.* (1978) noted that ethylene production by young bolls was low early in the season when boll abscission rates were low and

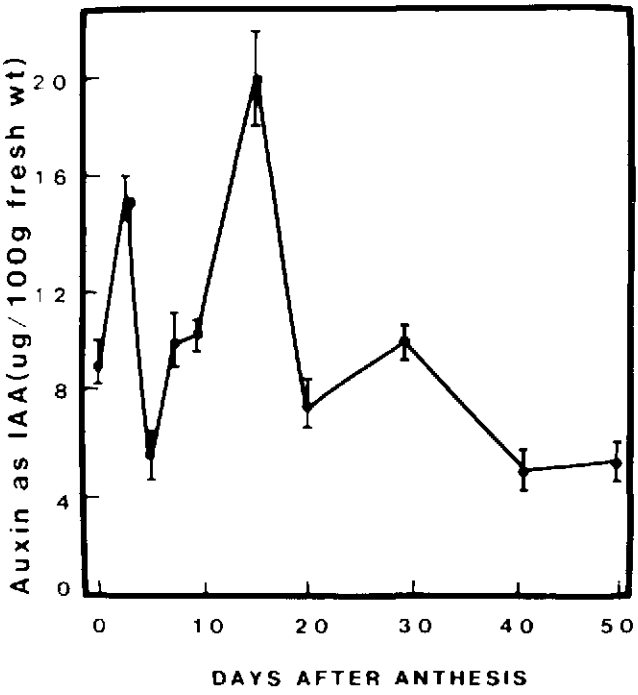

Figure 1. Variation in auxin concentration during the development of retained cotton fruit. (Each point is the average of 3 replications and the vertical lines represent ± SE. Data of Rodgers, 1981a, by permission).

then increased during the season and between irrigations as boll abscission rates increased. Guinn (1982a) investigated the changes in ethylene evolution with boll age and in response to dim light and wounding. Peak rates of ethylene evolution occurred at 4 days after anthesis in control bolls (Figure 3) and at 6 days in bolls of plants exposed to dim light. Dim light caused a considerable increase in ethylene evolution and 100 percent abscission of bolls up to 6 days old. Both ethylene evolution and rate of boll abscission were lower in bolls that were older when exposed to dim light. Wounding, caused by slicing the bolls, induced very high rates of ethylene evolution, but the rate declined markedly with boll age. These results suggest that the capacity for ethylene production declines with boll age, and this may be one factor that causes older bolls to be more resistant to shedding. Changes in other hormones and an increase in woodiness of the peduncle are also likely factors in causing a decrease in abscission with increasing boll age.

Cognée (1975) estimated the gibberellin content of bolls for the first 4 or 5 days after anthesis. He found minimum amounts at or 1 day after anthesis and maxi-

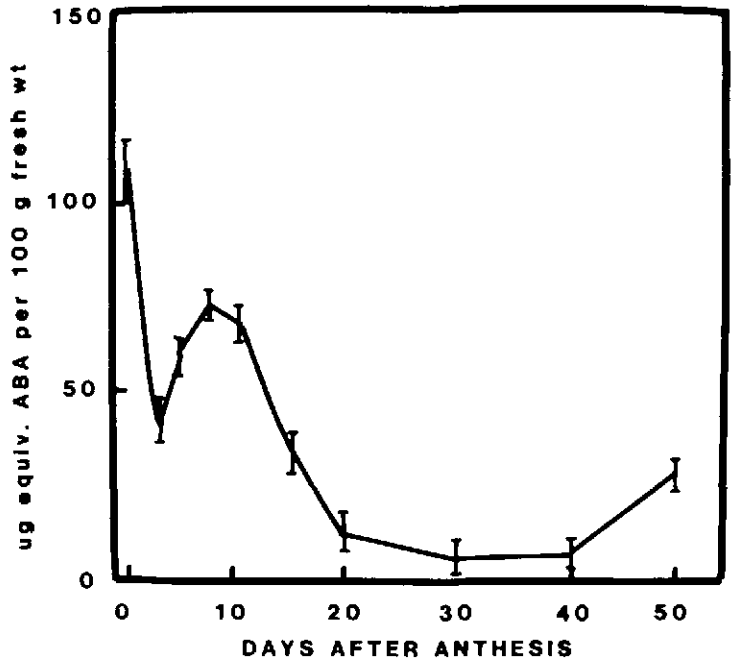

Figure 2. Changes in the concentration of ABA-like activity during the development of cotton fruit. (Data are averages of 3 tests and standard errors are shown. Data of Rodgers, 1980b, by permission).

mum amounts 2 to 5 days after anthesis. Rodgers (1981c) measured gibberellin activity at intervals from anthesis to 50 days later. He found maximum concentrations at 3, 15 and 50 days and minimum concentrations at 7 and 40 days after anthesis (Figure 4).

Cytokinin content of bolls also increases after anthesis. Sandstedt (1971) separated the cytokinins from cotton bolls by paper chromatography into two fractions. One fraction increased to a maximum 5 to 6 days after anthesis and then disappeared by the time bolls were 15 days old. The other fraction remained constant at a relatively low level through day 6 and then declined to unmeasurable amounts by day 18. Rodgers (1982b) reported peaks of cytokinin activity at 5 and 15 days after anthesis (Figure 5). His results differed from those of Sandstedt (1971) in that Sandstedt did not find high cytokinin activity 15 days after anthesis.

Boll abscission rate not only changes with boll load, it also changes with boll age (Guinn, 1982a). To obtain more precise data on changes in abscission rate with boll age, we tagged flowers at anthesis during July, 1981. Abscised bolls were gathered daily, except for Saturdays and Sundays, and counted. Mondays were

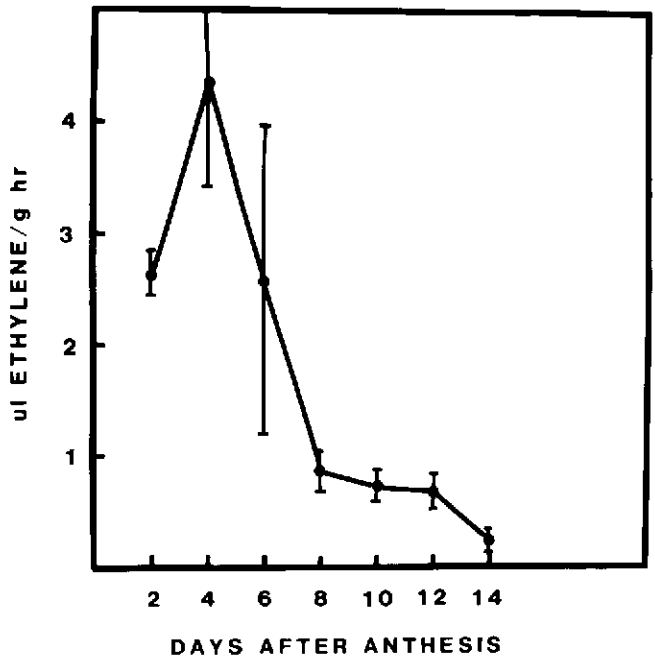

Figure 3. Ethylene evolution from young cotton fruits as influenced by fruit age. (Data are averages of 4 replications of two or more fruits per sample and standard errors are shown. Data of Guinn, 1982).

treated as a cleanup day. Boll abscission was calculated as a percentage of all bolls in that age group which abscised at that age. Abscission rate was very low the day after anthesis but increased rapidly to a peak at 5 to 6 days after anthesis (Figure 6). The rate declined as bolls became older and reached a very low level at 18 days after anthesis. Rodgers (1980a) reported similar results except that he found peak rates of shedding at 5 and 10 days after anthesis.

If one assumes that the abscission process requires a day or two for completion, it seems logical to assume that the effective growth regulator should show a change before a change in abscission rate. The peak rate of ethylene production preceded the peak rate of abscission (cf. Figures 3 and 6), and the rates then declined in parallel. ABA content reached a maximum after the peak abscission rate (cf. Figures 2 and 6). Low concentrations of auxins and gibberellins coincided with high rates of boll abscission (Figures 1, 4 and 6). Except for the large peak at 15 days after anthesis, cytokinin-like activity was at a maximum at the boll age of maximum abscission (cf. Figures 5 and 6).

The interaction of plant growth regulators may be more important in controlling boll abscission than the concentration of any one alone. High concentrations of auxin (Rodgers, 1981a) and gibberellins (Rodgers, 1981c) at 3 days after anthesis (Figures 1 and 4) may counteract the abscission promoting effects of

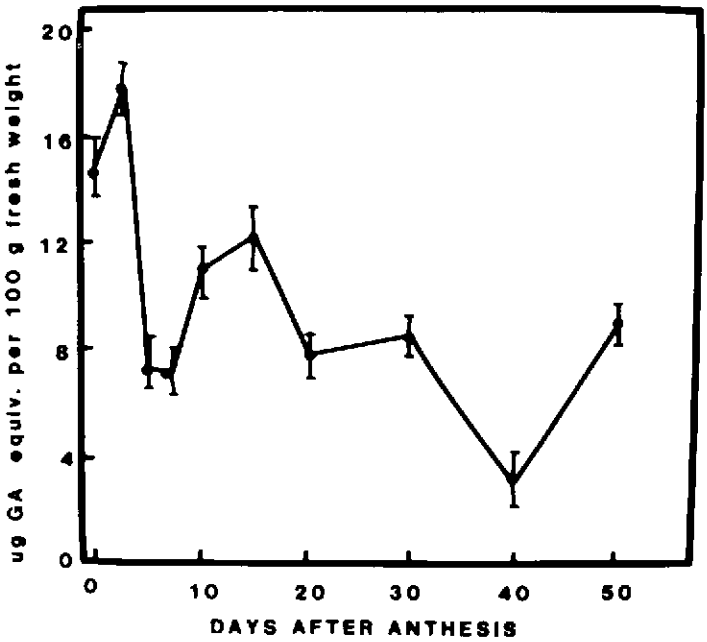

Figure 4. Changes in the levels of GA-like substances during development of the cotton fruit. (Each point is the mean of 3 values and vertical bars represent standard errors of the means. Data of Rodgers, 1981c, by permission).

relatively high ethylene evolution at, and shortly after, anthesis (Lipe and Morgan, 1972a). High concentrations of auxin (Rodgers, 1981a), gibberellins (Rodgers, 1981c) and possibly cytokinins (Rodgers, 1981b) at 15 days after anthesis, in addition to a declining concentration of ABA (Davis and Addicott, 1972; Rodgers, 1980b; Guinn, 1982a) and a declining capacity for ethylene production (Guinn, 1982), may combine to contribute to the marked decline in boll abscission rate at that age (Figure 6).

More information is needed on sequential changes and interactions of hormones during the season as they influence cutout, not only in fruits but also in growing points. We also need more information on effects of environment on hormonal balance and on possible differences between determinate and indeterminate cultivars.

EXOGENOUS MODIFICATION

In addition to greenhouse, growth chamber and laboratory tests on effects of various growth regulators, several investigators have tested growth regulators on field-grown cotton. The goals of these tests have been to increase boll retention

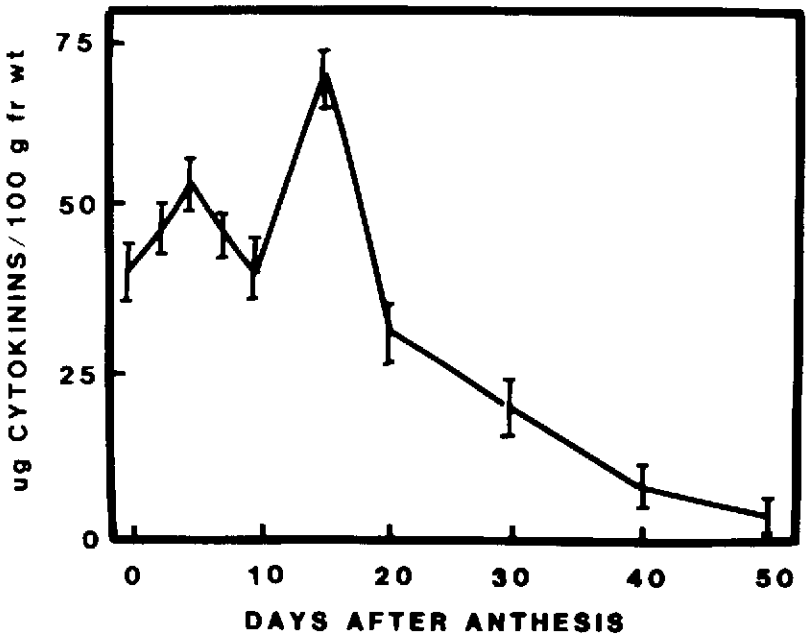

Figure 5. Changes in the concentration of cytokinin-like substances in lint and seed of developing cotton fruit. (Each point is the mean of 3 replications and standard errors of the means are indicated by vertical bars. Data of Rodgers, 1981b, by permission).

and yield, to limit growth of plants, or to remove squares and young bolls and terminate growth and fruiting activities (see Chapter 13).

Freytag and Coleman (1973) applied 2, 3, 5-triiodo-benzoic acid (TIBA) to two cultivars of cotton during 2 years in a field test at Lubbock, Texas. Application of TIBA tended to lower the position of the first fruiting node, increase boll size and increase the number of bolls per plant. After combining the data for both cultivars for both years, they calculated yield increases of up to 16 percent for the most effective treatment, 5g/ha applied five times. They postulated that TIBA inhibited auxin (IAA) transport and decreased endogenous ethylene concentration. However, inhibition of auxin transport should promote, rather than inhibit, abscission.

Application of gibberellins (GA) directly to open flowers or young bolls increased the percentage of bolls retained (Walhood, 1957, 1958). The optimum concentration appeared to be about 100 ppm. Attempts at increasing yields by field applications of GA have been disappointing. Lane (1958) reported that plants treated with GA on the Texas High Plains seemed somewhat larger, but their yield was slightly less than that of the controls. Walhood (1958) applied GA

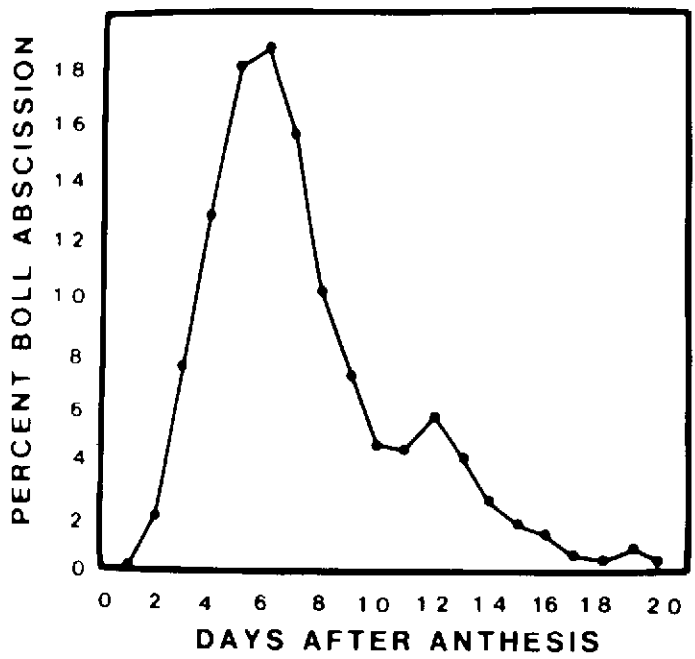

Figure 6. Fruit abscission rates during July as a function of fruit age. (Each point represents a population of 1,460 to 4,480 fruits. Previously unpublished data of Guinn).

by airplane and by hand in California. Application by plane gave slightly higher yields in some cases, but the results were erratic and showed no relationship between rate of application and yield increases. He applied GA at the rate of 0.61 g/ha directly to the growing points of plants either once or several times during the fruiting season. Application of GA to the growing points increased plant height and the number of bolls produced, but the bolls were smaller. Application of GA increased yields on a light soil where the untreated plants quit growing and fruiting during mid-summer but did not affect yield on a heavier soil where plants grew and fruited for a longer time. The beneficial effect may have been related to stimulation of growth and delay of cutout. Walhood (1957) reported earlier that application of GA to the terminals of cotton plants that had cutout caused them to resume growth. Subbiah and Mariakulandai (1972) found that GA and naphthalene acetic acid (NAA) decreased abscission of squares and bolls, but they were unable to increase yields by spraying cotton plants with GA and NAA. Their untreated controls produced the highest yields.

A few reports indicate that NAA may increase boll retention and yield. Negi and Singh (1956) applied NAA at 5, 10 and 20 ppm and reported an increase in

the number of bolls and yield in the first picking. Their data show an 8 to 9 percent yield increase with 10 ppm NAA applied as foliar spray but a slight decrease the number of bolls and yield in the first picking. Their data show an 8 to 9 percent yield increase with 10 ppm NAA applied as foliar spray, but a slight decrease with 20 ppm NAA. Murty *et al.* (1976) claimed a 50 percent decrease in boll shedding and a 20 to 35 percent increase in yield after spraying cotton plants with 10 and 30 ppm NAA. They concluded that spraying with 30 ppm NAA at the initiation of flowering and again at the time of peak flowering would decrease boll shedding and increase yields. Varma (1976) reported that application of NAA to flower buds, bolls or boll explants completely counteracted the abscission-promoting effects of ABA.

Many reports have shown that application of IAA or NAA to explants distal to the abscission zone delays and inhibits abscission, but proximal applications usually promote abscission unless applied at rather high concentrations (Addicott and Lynch, 1955; Addicott, 1970). It is possible that foliar application of IAA or a synthetic auxin, such as NAA, may indirectly affect abscission and yield by stimulating photosynthesis. Turner and Bidwell (1965), Bidwell and Turner (1966) and Tamas and co-workers (1972, 1974) obtained evidence that IAA stimulated photophosphorylation and CO_2 fixation in isolated chloroplasts and leaves.

Growth retardants have been used in an attempt to limit excessive vegetative growth of cotton. Singh (1970) applied (2-chloroethyltrimethylammonium) chloride (also known as CCC, Cycocel, and chlormequat) to three cultivars of *G. hirsutum* and one cultivar of *G. arboreum* growing in field plots in Punjab, India, where excessive vegetative growth was a problem. Application of CCC 70 to 80 days after planting retarded growth and increased the number of bolls per plant, boll weight and yield. Sprays of 40 ppm CCC increased yield of the *G. hirsutum* cultivars by 18 to 45 percent and sprays of 160 ppm CCC increased the yield of *G. arboreum* 15 to 34 percent. Singh also found evidence that CCC promoted drought resistance at Abohar.

Other workers were able to limit growth with CCC but did not find any yield increases; on the contrary, early application or high rates decreased yield (Thomas, 1964, 1967, 1975; Zur *et al.*, 1970, 1972; Marani *et al.*, 1973). Marani *et al.* (1973) applied CCC at 50 and 100 g/ha and applied N-dimethyl-N- β -chlorethyl-hydrazonium chloride (CMH) at 480 and 720 g/ha. Both growth retardants significantly decreased the growth rate. When applied at the beginning of flowering, neither CCC at 50 g/ha nor CMH at either rate decreased lint quality or yield. El-Baz *et al.* (1971) and Thomas (1972) were also able to limit plant height with CCC without causing significant yield reductions. Application of CCC at 100 g/ha did decrease yield, possibly because of decreased boll retention (Marani *et al.*, 1973). Thomas also reported decreased boll set (1964, 1975) on plants treated with CCC.

Another growth retardant, 1,1-dimethylpiperidinium chloride (also known as mepiquat chloride or Pix), has been tested rather extensively in recent years. Most of the results have been reported at the Beltwide Cotton Production Re-

search Conferences and published in the Proceedings. Pix rather consistently decreases plant height and leaf area, and causes leaves to be thicker (e.g., Walter *et al.* 1980). It sometimes increases yield but yield responses have not been consistent. Yield increases may result from more favorable light penetration when plants would grow tall and rank without the growth retardant. Application of Pix also tends to promote earliness in some cases (Briggs, 1981) but not in others (Crawford, 1981).

Under some circumstances it may be desirable to delay first bloom or to decrease the percentage of squares that produce blooms. Pinkas (1972) used (2-chloroethyl) phosphonic acid (ethephon) to cause abscission of first squares in order to raise the position of the first bolls on Pima S-4. This facilitated mechanical harvesting in an area where this cultivar tended to fruit close to the ground. Prokef'ev *et al.* (1977) reasoned that less assimilate would be lost if superfluous fruits were abscised as young squares rather than young bolls. They treated plants with 2-mercaptoethanol (MET) and N, N-dimethylmorpholinium chloride (DMC) to prevent the formation of excess fruits or to destroy them at the stage of rudimentary buds. Treatment with 0.1 and 0.5 percent MET decreased yield, but treatment with DMC increased earliness and yield. They reported that spraying with DMC increased yield in the first picking by 66 to 73 percent, increased boll weight about 1 gram, and increased total yield 26 to 30 percent. The lowest concentration was almost as effective as the highest over the range tested, 0.046 to 0.45 percent.

Kittock and Arle (1977) used CCC and other growth regulators to terminate fruiting. Their goal was to remove squares and small bolls late in the season to deprive pre-diapausing pink bollworm larvae of a food supply. They identified two types of action: fast-acting nonpersistent and slow-acting persistent. A mixture of growth regulators with each type of action gave the most effective chemical termination of fruiting. The slow-acting persistent regulators included CCC and chlorflurenol (methyl 2-chloro-9-hydroxyfluorene-9-carboxylate). The fast-acting growth regulators included 2,4-D (2, 4-dichlorophenoxyacetic acid) and 3,4-dichloroisothiazole-5-carboxylic acid.

SUMMARY

Modern varieties of cotton flower readily without special photoperiods or hormonal modification. Therefore, little research has been done on the role of hormones in flowering and little is known about their effects on flower induction.

Much more is known about the roles of hormones in abscission. In order for abscission of cotton bolls to occur, cell walls in the abscission zone must be weakened by the hydrolytic enzymes pectinase and cellulase. The abscission-promoting hormones, ethylene and abscisic acid, have been reported to stimulate synthesis of cellulase and to decrease the basipetal movement of auxin (indole-3-acetic acid) to the abscission zone. Auxin normally delays or prevents abscission,

possibly because it prevents the synthesis and secretion of the specific cellulase involved in abscission. Gibberellins promote abscission of explants (isolated portions of plants) but inhibit abscission when applied to cotton flowers or young bolls. Cytokinins have variable effects and may either promote or retard abscission, depending upon time and site of application. The effects of gibberellins and cytokinins may be due mainly to their ability to mobilize nutrients to the site of their application or natural distribution.

Relatively little is known about hormonal control of cutout, but based on established effects of the hormones, we can speculate that auxin, cytokinins and gibberellins promote growth and delay cutout. ABA, on the other hand, probably promotes cutout because it inhibits growth and prolongs bud dormancy. Ethylene increases boll abscission and may restrict growth, but it probably does not prolong bud dormancy. Bolls may affect cutout by producing ABA and by competing with shoot and root growing points for sugars and nitrogenous compounds. This competition could affect hormonal balance by affecting the production of hormones and by decreasing the uptake of water and inorganic nutrients from the soil. A decrease in nitrogen content of roots and shoots could decrease the synthesis of auxin and cytokinins and increase the production of ABA. ABA content has been shown to increase in response to water and nitrogen deficits.

Various growth regulators have been applied to cotton in attempts to set more bolls, limit vegetative growth, or terminate fruiting. When boll load is limited by carbohydrate supply, exogenous modification of hormonal balance to increase boll set may be futile. More bolls may be set, but they will probably be smaller and the plants may cut out sooner. If, however, the growth regulators stimulate photosynthesis, boll set and yield may be increased. Hormonal control of plant height is possible and may be a useful practice when rainy weather and insect pests cause excessive growth that can result in lodging and boll rots. Hormonal termination of growth and fruiting appears to be a useful method of depriving prediapause insect pests of food and, thereby, of limiting the number that survive the winter.

Short-season techniques are currently being promoted to decrease production costs and minimize late-season and overwintering insect problems. The ability to control flowering, fruiting and cutout is essential, if maximum yields are to be obtained. A more detailed and thorough understanding of the physiology of the cotton plant should enable us to do a better job of tailoring plant performance to fit specific needs and situations.