

Chapter 2

VEGETATIVE GROWTH AND DEVELOPMENT OF FRUITING SITES

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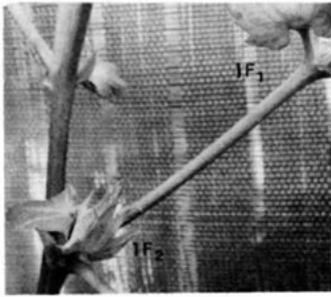
INTRODUCTION

The cotton plant has perhaps the most complex structure of any major field crop. Its indeterminate growth habit and sympodial fruiting branch cause it to develop a four dimensional occupation of space and time which often defies analysis. The research reported in this review is representative of the attempts to quantify the physiology of the production of the fruiting sites which ultimately lead to lint and seed. Though the older studies used obsolete cultivars and cultural practices, the data may be taken as indicative of the trends in modern cultivars and practices. However, caution is appropriate in the use of field data about fruiting patterns. No research has been conducted in fields of cotton which were free of insects and diseases; no such fields exist. Therefore, to some extent these stresses always confound our interpretations of the physiological processes which produce fruiting sites. However, awareness and caution should reduce our chances for confusion.

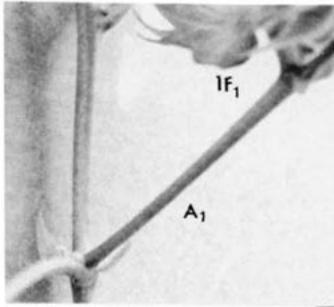
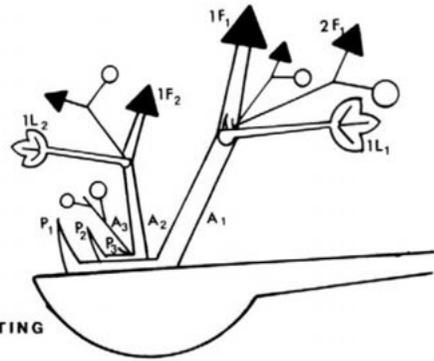
MORPHOLOGICAL DEVELOPMENT

The morphological development of the cotton plant leading to production of flower buds (squares) was reviewed by Hector (1936) Tharp (1960) and Mauney (1968, 1984a). The essentials of this process are that the primary axis of the plant remains vegetative throughout the life of each individual plant. Axillary branches differentiate at the base of each leaf on the plant and these branch axes are responsible for all vegetative limbs (monopodia) and reproductive branches (sympodia). Schematic representation of typical branch structures is shown in Figure 1.

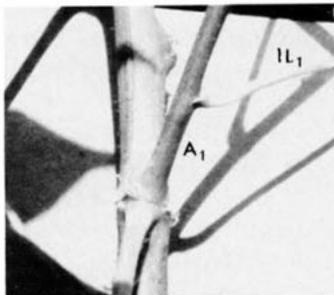
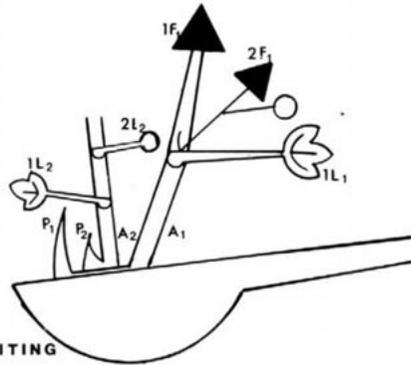
There are usually two branch buds at the base of each leaf. Mauney and Ball (1959) designated the more-prominent of the buds the "first" axillary and the slower-developing one the "second" axillary. They studied the anatomical relationship of these buds and found the second axillary to be a branch off the first axillary. This relationship is important because it influences the tendency of the



UPPER NODES: EXCEPTIONAL FRUITING



INTERMEDIATE NODES: TYPICAL FRUITING



LOWER NODES: VEGETATIVE

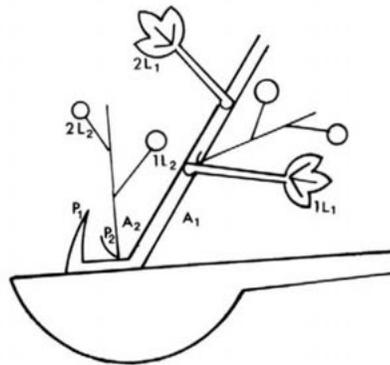


Figure 1. Photographic and schematic representations of vegetative and fruiting axillary branches from low, intermediate and upper nodes of a plant.

 —expanded true leaves (L),  —unexpanded true leaves (L),  —prophylls (P),  —flower buds (squares) (F). Numerals refer to the position of the organ along the branch, subscripts refer to whether the organ is on a first (A_1), second (A_2), or third (A_3) axillary. Thus, $1L_1$ is the first true leaf of the first axillary, $2F_2$ is the second flower of the second axillary, etc.

buds to produce flowers. At low nodes on the main stem the first axillaries are vegetative and may elongate into vigorous vegetative limbs (Figure 1 Vegetative). When the plant is induced to flower, the first axillary becomes a fruiting branch and the second axillary remains vegetative and usually dormant (Figure 1 Typical Fruiting). Once induced, the plant seldom reverts to producing vegetative buds at the first axillary position. This does happen, however, and occasionally there will be one or more vegetative limbs above the first fruiting branch.

At higher nodes the plant may become vigorous in reproductive development and produce floral branches at both the first and second axillary (Figure 1. Exceptional Fruiting). Although these second axillary floral branches are usually short spurs which produce only one flower, they are potentially important sites for additional bolls. The second axillary position at the base of each square on the sympodium may also develop into a square. Thus, in vigorously-flowering plants, each sympodium may bear twice as many squares on a given number of nodes as in less-vigorous plants.

VEGETATIVE GROWTH

Since all reproductive branches arise at the base of vegetative leaves, the initiation and the rate of formation of sympodia are partially dependent upon vegetative growth. Mauney (1966), Zaitzev (1928), and Hesketh *et al.*, (1972) have shown that the rate of vegetative growth prior to onset of flowering is temperature-dependent. Hesketh *et al.* (1972) observed that the plastochron (days between successive organs) for leaves was three times as long at 18C as at 30C. At 30C they found the leaf plastochron to be 2.2 days.

Though the rate of production of new vegetative leaves—and therefore new fruiting branch sites—is highly dependent on temperature, it is also very sensitive to water stress. For that reason the rate of vegetative leaf growth cannot continue the exponential increase which it exhibits during the seedling and juvenile stages of plant development. At some point the leaf area begins to exceed the capability of the root system to explore new soil volume or to absorb and transport water to the stomates. The point at which growth reduction will be observed will depend on complex soil, weather, and plant interactions, but it is certain to occur. The familiar sigmoid growth curves of all organisms are based on the certainty that an exponential increase in size can continue for only a relatively short period before some resource becomes limiting. In the case of cotton seedlings, uptake of water probably becomes that limiting factor (Mutsaers, 1983b; also see Chapter 10).

Upon germination the root system of the seedling develops more rapidly than the leaf area which is limited to cotyledon expansion. True leaf expansion is delayed by the fact that cotton has no plumule above the cotyledons in the germinating seed (Mauney, 1984a). The root system continues to expand during the 7 to 10 days in which the true leaves differentiate and develop up to expansion of the first true leaf. The first five true leaves are progressively larger in mature area. Thus, the leaf area equivalent for each node of the stem increases as growth

continues. Branch primordia are more active at about the fifth node, and first vegetative and then fruiting branches form secondary leaves. This means that the leaf area equivalent for each stem node increases from the first to about the tenth node. (Mutsaers, 1983b)

Assuming that the roots are growing into a soil profile at field capacity, at some point in the progression of seedling growth the root area/leaf area ratio will reach a maximum and then decline to a level at which root expansion into wet soil matches leaf area expansion. If additional water is then added to the soil through rain or irrigation there will be a temporary increase in growth. Growth cannot exceed the capability of roots to absorb and transport water. Significantly, in a glasshouse experiment (Mauney *et al.*, 1978) growth, as measured by rate of addition of primary leaves, began to decline two weeks prior to appearance of the first blossom (Figure 2). These plants were never visibly stressed for water or

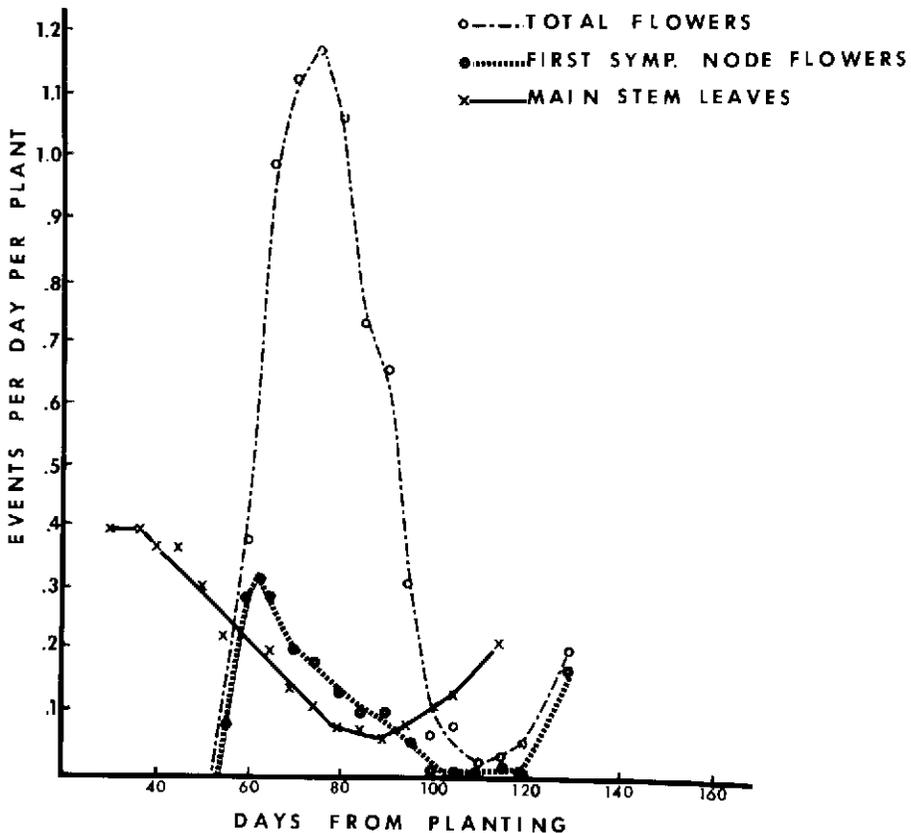


Figure 2. Rate (expressed as number appearing per day) of leaf and flower development with age of cotton plants grown under glasshouse conditions in Arizona (see Mauney *et al.*, 1978 for conditions).

mineral nutrients. As seedlings they achieved the plastocron predicted by Hesketh *et al.* (1972) but declined in growth rate long before carbohydrate competition by bolls became a factor.

Guinn and Mauney (1983a) observed that delaying the first irrigation until two weeks after the first square was visible did not reduce the initial rate of flowering in Arizona. This water stress did reduce the rate of vegetative growth but in some years the number of flowers in the first two weeks of flowering was greater in the water stressed treatments than in the well-watered plots. The increase in early flowering was in years in which there was a significant population of plant bugs (principally *Lygus* species). They concluded that fewer squares were shed in the water stressed plots because the plants were less attractive to plant bug feeding.

Restrictions in growth due to severe water stress after onset of flowering have generally been found to reduce yield (Grimes *et al.*, 1970; Guinn and Mauney, 1983b). Although water stress caused some square shedding and a reduction in boll retention, Guinn and Mauney (1983a) found that the principal cause of reduction of yield was the reduction in numbers of flowers three weeks after the severe water stress. The reduction in flower numbers is a measure of the effect of water stress on vegetative growth and production of new fruiting branches.

INITIATION OF FLOWERING

Though initiation of flowering in modern cultivated cottons is not significantly influenced by photoperiod (Mauney and Phillips, 1963), there are environmental influences on the process. Mauney (1966) observed that differentiation of the first floral bud could begin as early as 10 to 14 days after emergence. At this stage of growth the plant will have two or three expanded true leaves. The removal of these leaves will delay flowering (Mauney, 1963). The day and night temperature and the quality and intensity of light during this stage of plant development can change the placement of the first fruiting node.

The length of time between planting and development of the first square and flower depends also upon the node at which the first fruiting branch appears (NFB). At lower temperatures the NFB is lower (Mauney, 1966; Moraghan *et al.*, 1968; Low *et al.*, 1969; Hesketh *et al.*, 1972). NFB was 6 when plants were grown at 26C/23C (day/night) but was 10 when plants were grown at 32C/29C. Because of the complex interaction of growth rate and node of initiation, the time from emergence to first square may be shorter at certain cool temperature regimes than at higher temperatures.

In field plantings, however, cool temperature is a primary reason for delay in both first square and first flower. Constable (1976) found that a 4-week delay of planting caused only a 1-week delay of the date of first flower (DSF). This was due primarily to the shorter time from seedling emergence to first square at the higher temperatures of the later plantings. He calculated the growing degree days (GDD) for the period of planting to first flower. Using 14C as the base, his GDD for this period was 647. Bilbro (1975) also observed that DSF was not delayed

equally with a shift in planting date. DSF was delayed only 2 days because of a 3-week delay of planting. He calculated a GDD of 621 using a base temperature of 14C. Mahon and Low (1972) used 10C as the base for their calculations and found GDD to be 880-900 from planting to first flower. This converts to about 650 if the base is 14C. Anderson (1971a) found that delay of emergence by low temperature was poorly correlated ($r^2 = .25$) with the number of days to first square in five varieties which differed markedly in maturity classification.

FLOWER DEVELOPMENT

After initiation, the continuation of flowering is, of course, a function of vegetative growth which produces sites for additional fruiting branches and of

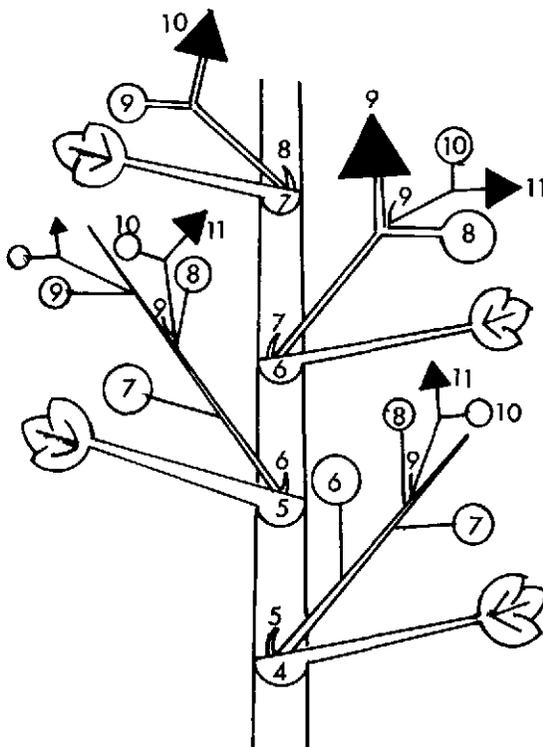


Figure 3. Schematic representation of a main stem axis in transition from vegetative branching to reproductive branching. This plant had the first flower from the branch at node 6. The numerals represent succession of leaf units (true leaves, ; prophylls, ; and bracts of squares, ). Though the leaf units are not precisely equal in time length (isophase), they are approximately 2.5 to 3.0 days. Events with the same leaf unit number should occur within a few days.

formation of additional nodes on existing branches. Both of these rates of node production are temperature dependent (Hesketh *et al.*, 1972): the rate at 30C was three times faster than it was at 18C. The base rate at 30C for successive initiation of additional fruiting branches, vertical flowering interval (VFI), was 2.0. The rate of adding successive nodes along a fruiting branch, horizontal flowering interval (HFI) was 6.0. Other workers have observed VFI to range between 2.2 and 4.0 and HFI to range from 5.8 to 8.5 (McClelland and Neely, 1931; McNamara *et al.*, 1940; Kerby and Buxton, 1978). Zaitzev (1928) argued that a relationship which he termed "isophases" should exist between the HFI and the VFI. Most observers have calculated the ratio HFI/VFI to be near 2.5 (Mutsaers, 1983a).

The reason that HFI is more than twice VFI can be seen by examining the net number of morphological events which separate the flowers in these two planes. Figure 3 shows development of a plant in the transition zone in which the plant shifts from vegetative branching to floral branching. By counting the sequence of developmental structures we see that there is a net of only one structure, the main stem internode, between successive flowers in the vertical plane. This is because all structures at successive nodes along the main stem can develop simultaneously, separated in age only by the time required to develop the internode. In the horizontal plane, on the other hand, both the prophyll and the subtending leaf must develop prior to differentiation of successive flowers. This means that at least two events separate flowers in the horizontal plane. The fractional nature of the prophyll event may account for the fact that the ratio of HFI to VFI does not calculate to an even number as Zaitzev expected that it should.

With onset of fruiting, an additional growth factor complicates the rate of addition of new sympodia. The plant slows production of main stem leaves, presumably because of the competition for carbohydrate from the developing bolls.

Baker *et al.* (1972; also see Chapter 19) developed computer simulations of cotton plant growth in which the supply:demand ratio for carbohydrate controlled the growth rate of the various plant parts. Using this program they were able to simulate the decline in growth of main stem nodes (MSN) which occurs with onset of fruiting.

Unpublished data from the glasshouse experiments described by Mauney *et al.* (1978) illustrate the decline of vegetative growth (Figure 2). These observations were made in maximal sunlight, optimum temperature (35C/22C, day/night, throughout) and no water or nutrient stress. In this optimum environment the rate of production of new MSN (and therefore additional sympodia) began decreasing with the onset of squaring. Shortly after the onset of blossoming the rate of flower opening (inverse of VFI) exceeded the rate of new leaf formation. The inevitable result of this excess of flower opening over new leaf and sympodia formation was that the flowers opened at nodes closer and closer to the apex of the stem. In time, the plants expended the positions available and flowering stopped. Renewed

growth of the vegetative apex then produced new floral sites and blossoming resumed—after a hiatus.

Cessation of flowering is, of course, cut-out. The fact that it occurs even in the absence of environmental stress indicates that it is a basic pattern of growth for the cotton plant. However, genetic background and environmental stress undoubtedly influence the magnitude of the excess of flower opening to new leaf and sympodium formation and, thus, both the timing and the severity of the cut-out phenomenon.

In field experiments, Kerby and Buxton (1978) observed a slight increase in VFI during the first 30 days of flowering. In Figure 5 their data are plotted with VFI observations from our glasshouse study and additional (unpublished) data from field plantings in 1976 in Arizona. The trend in each of these experiments was the same, toward greater VFI as the season progressed.

Temperature is a confounding factor in field observations and might largely account for the differences in average VFI among years. However, the increases in VFI with seasonal progression in the field are very much like those observed in the glasshouse where temperatures did not change throughout the experiment. This suggests that the greater VFI is due to a slowing of growth in the field which is similar to that observed in the glasshouse.

The fact that the total flowers per plant per day also reaches a peak and then decreases to near zero (Figure 2) implies that the sympodia are limited in length

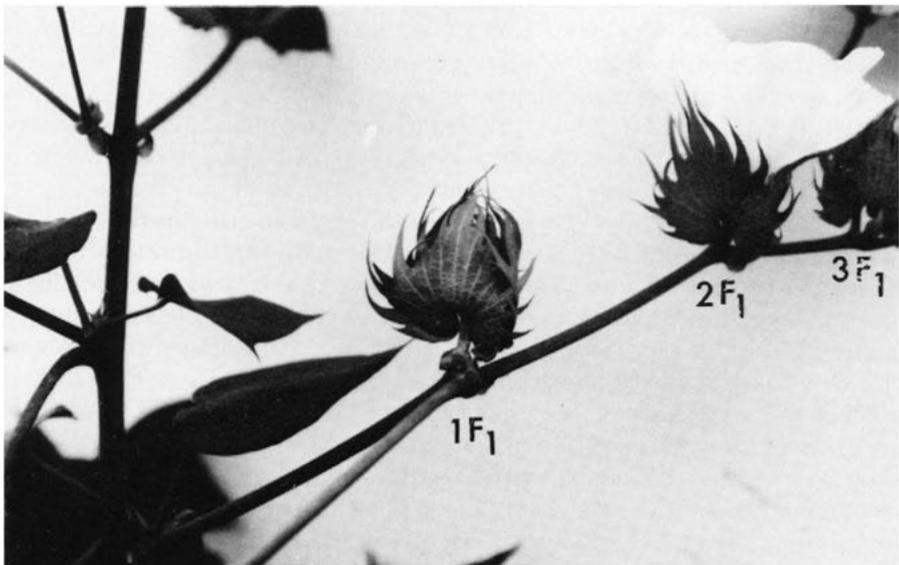


Figure 4. Prime sites for harvestable bolls are the first three flowering positions along each branch. Shown here are a boll at the first node ($1F_1$), a flower at the second node ($2F_1$) and a square at the third node ($3F_1$).

and that HFI becomes greater as the season progresses. This was observed to be the case (Figure 5 HFI-GH). For comparison, the data of Kerby and Buxton (1978) and unpublished data from this laboratory from field plantings in 1976 are plotted in Figure 5. The failure of Kerby and Buxton (1978) to observe a significant shift in HFI may be due to the longer initial HFI which they observed (due apparently to low temperature, particularly in 1974). Further, their observations did not extend into the latter portion of the flower production season when increased HFI is most apparent.

Hesketh *et al.* (1972) reported temperature effects on rate of square maturation (square period) which were similar to those calculated for other organs. i.e. the rate at 39C was three times that at 18C. The square period at 30C was 22.5 days. Other workers have observed square periods of 23 days, (Martin *et al.*, 1923), 22-30 days (Beckett, 1927) and 20-23 days (Brown, 1938).

Since a longer square period could account for some of the increase in VFI and HFI plotted in Figure 5, I have examined unpublished data from the glasshouse experiments described by Mauney *et al.* (1978). In these experiments, in which average daily temperature was 29C, the square period was 21.6 days and did not change significantly from the first to the last square produced. Matthews (1978) reported that, in Arizona, squares produced on sympodia at main stem node 10 took 5 days longer to mature into blossoms than those from branches at main stem node 15. Increasing temperatures in June may have influenced the shorter square period of the higher nodes. Hintz and Green (1954), on the other hand, observed that squares appearing in August in Oklahoma had about 1 day longer square period than those appearing in July. Lower August temperature was probably the cause of this slower growth.

The implication of these findings is that, although production of squares up to visible size (*ca.* 3mm.) is a function of vegetative growth (which, in turn, is sensitive to boll load as well as temperature and other stresses), the growth of the square after it becomes visible is not sensitive to growth of the vegetative organs of the plant. This conclusion further implies that visible squares are either photosynthetically self-sufficient or are sufficiently powerful as sinks that the limited amount of carbohydrate needed for their growth can be supplied by the plant even during stress. The conclusion of Hearn (1969) that sympodial growth is limited by competition for light would seem to indicate that squares (at least those several nodes out on sympodia) are not able to draw carbohydrate from distant leaves. Although these data are not definitive, they would seem to favor the hypothesis that squares are primarily self-sufficient. (See Chapter 20 for other aspects of square development).

PRIME SITES OF FRUITING

Tharp (1962) calculated that in 10 weeks from the first bloom a cotton plant could produce 156 flowers without considering vegetative branches. This estimate is too high for several reasons. The principal error was the assumption that

fruiting branches would continue to elongate indefinitely. The longest branches in Tharp's model had 12 nodes. This number of nodes is seldom observed in field plantings. In dense stands the first fruiting branches soon become shaded and either cease growing or shed a large proportion of the squares or fruit which are initiated.

Table 1 lists observations of the placement of harvestable bolls covering more than 50 years of experimentation on widely differing cultivars and locations. Invariably, greater than 80 percent of all yield has been found at the first ($1F_1$ in Figure 4) and second ($2F_1$ in Figure 4) nodes on the fruiting branches. The agreement among these data indicates a basic physiological limitation of the positions beyond the first two nodes on each fruiting branch. Mathews (1978) and Kerby and Buxton (1981) have observed a somewhat greater tendency of the $2F_1$ position to retain a harvestable boll if $1F_1$ has been lost. However, in no case did

Table 1. Placement of harvestable yield by percentage at each node on fruiting branches.

Reference	Location	Yield at fruit branch node			Lint yield (kg/ha)
		$1F_1$	$2F_1$	Other	
McNamara <i>et al.</i> (1940)	Texas	56	26	18	ca.300 ¹
Munro (1971)	Africa	62	32	6	1030
Mauney <i>et al.</i> (1978)	Greenhouse	43	32	19	1740
Mauney—unpubl—1976	Ariz.	71	26	3	
Mauney—unpubl—1977	Ariz.	76	20	4	
Mauney—unpubl—1978	Ariz.	74	22	4	900
Mauney—unpubl—1980	Ariz.	76	18	6	1200
Mauney—unpubl—1981	Ariz.	59	25	16	1850
Kerby & Buxton (1981)	Ariz.	76	16	8 ²	
Kerby—unpubl—1982	Calif.	69	27	4	

¹Yield from variety tests at Greenville, Texas 1931-38

²Includes all bolls matured on vegetative branches as well as at nodes three and greater on fruiting branches.

this compensation change $2F_1$ into a boll retention pattern characteristic of $1F_1$.

Kerby and Buxton (1981) included all bolls on vegetative branches with those at positions greater than $2F_1$ on fruiting branches. They placed only 8 percent of harvestable yield in this category (Table 1). Mauney (unpublished) observed about 10 percent of harvestable bolls located on vegetative branches and that bolls on vegetative branches were almost exclusively at the $1F_1$ position. A photograph of bolls on a vegetative branch published by Hubbard (1931) shows all bolls located at $1F_1$ positions.

Hearn (1969) observed that as the density of planting increased the average number of fruiting points per main stem node decreased. At about 18,000 plants per acre he observed two nodes per sympodium of an indeterminate variety (BAR x L) and about three nodes per sympodium on a more rapidly fruiting determinate variety (Wild's Early). At a density of about 9,000 plants per acre, he observed about the same number of nodes per sympodium but about 50 percent more total squares per main stem node. Since his notation of squares per main stem node included all squares on vegetative limbs, he concluded that the principal effect of plant density was on the development of the vegetative limbs rather than on the length of sympodia. He contended that competition between adjacent plants determines the number of vegetative limbs and competition within each plant determines the length of fruiting branches. Apparently, after sympodia have developed three nodes, they are stressed by self shading and perhaps by nitrogen partitioning (see Radin and Mauney, Chapter 10) so that additional growth is limited and site productivity reduced to nil.

The number of sympodia which plants make in a season is influenced not only by the characteristics of the season, but also by the rapidity of new leaf development (leaf plastochron) and by the growth habit of the cultivar. Even relatively indeterminate cultivars such as DPL 16 begin to lengthen plastochron with onset of fruiting (Figure 5). Under ideal growing conditions in glasshouses Mauney *et al.* (1978) found that flowering reached a peak and then dropped to nil in about 60 days. Under such conditions, the plants produced 18 sympodia (unpublished data). Under less-favorable growing conditions, the initial flush of flowering may last longer, but plastochron will be longer and the total number of sympodial nodes will be changed very little. Matthews (1978) observed few sympodia at main stem nodes higher than 25 under irrigated conditions in Arizona. With severe temperature, nutritional, or moisture stresses, the growth of the plants will be restricted so that fewer sympodia will be produced.

If we accept that the first three nodes on each sympodium are the most likely sites for mature bolls, then 18 sympodia will produce about 50 prime square positions since the last few sympodia to develop will not have time to mature all three nodes. If 50 percent, 30 percent, and 10 percent of the squares at sympodial nodes $1F_1$, $2F_1$, and $3F_1$ respectively, mature into open bolls with 1.5 gms. lint per boll, 30,000 plants per acre would produce 1500 lbs. of lint per acre. Under favorable conditions this level of yield can be achieved before cut-out.

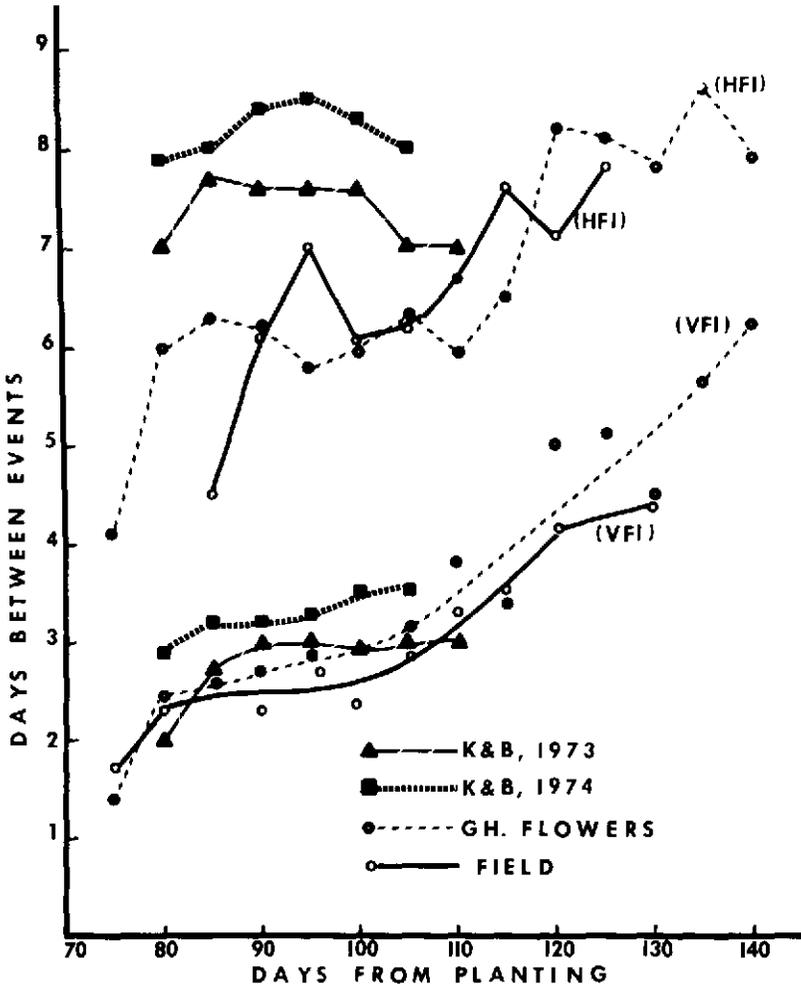


Figure 5. Rate (expressed as days between events) of flower development with age of cotton plants in field and glasshouses in Arizona. Vertical flower interval (VFI) in days between flower at the first node of successive fruiting branches. Horizontal flower interval (HFI) in days between flowers at successive nodes of the same fruiting branch. K&B is data from Kerby and Buxton (1978). Other data unpublished data of Mauney.

Graphic representations of average plants from plantings yielding 1000 and 2000 kg/ha (or lbs/ac) lint are shown in Figure 6 (Mauney, 1984b and unpublished). This representation depicts placement of bolls from field plantings in Arizona, but I believe it is fairly representative for other locations as well. The greater yield of the 2000 kg/ha planting was achieved by a greater number of main-stem nodes rather than utilization of more nodes per branch.

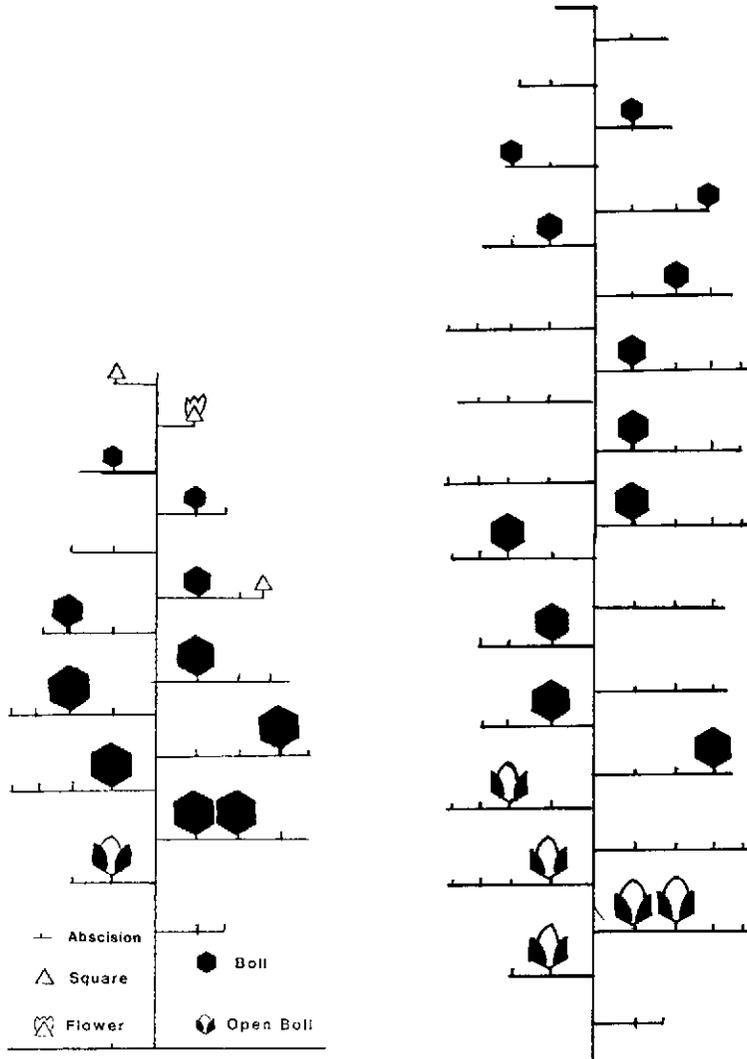


Figure 6. Schematic representation of boll locations on average plants from plantings yielding 1000 kg/ha (left) and 2000 kg/ha lint (right).

EARLINESS

“Earliness” in a cotton crop has several possible definitions. One that has been used is that of a high proportion of the crop harvested at first pick (Richmond and Radwan, 1962; Ray and Richmond, 1966). This definition has advantages when comparing varieties at a specified location, but it is obviously subject to extreme variation among locations and years.

Another definition of earliness is reaching an acceptable yield potential in the shortest time from planting. This concept was used by Munro (1971). He analyzed the components that would contribute to fewer days from planting to production of 30 fruiting points. The components of earliness he examined were DSF, NFB, VFI and HFI. In his analysis he used DSF=70, NFB=5, VFI=3.5 and HFI=10. He concluded that producing 30 fruiting points 9 days earlier could be accomplished by (1) advancing the DSF by nine days, (2) lowering the NFB by 2.0 nodes, (3) shortening the VFI by 1 day or, (4) shortening the HFI by 9 days. While changes of this magnitude are not practical for some of these characteristics, combinations of these changes would, of course, be additive in their effect on earliness.

Munro (1971) also observed that seven additional flowering positions on vegetative branches, reduction of fruiting point shedding from 60 to 46 percent or shortening the boll period by 9 days would similarly shorten the period for acceptable yield by 9 days. He considered that the most useful characters to modify by breeding were DSF and the boll maturation period. He analyzed the data of Mooseberg (1969) and found that more than half the earliness of an improved variety was due to these two characters.

In his analysis Munro did not consider one source of earliness that is under both genetic and cultural control; that is, the production of second axillary squares at nodes of the sympodia. From the previous discussion of the morphological relationships of the axils of both vegetative and sympodial leaves, it is obvious that these positions are available for differentiation into flower buds. There is genetic variability in the tendency of the second axillary to develop into a square or remain a dormant vegetative bud. *G. barbadense* varieties are more likely to develop second axillary flowers than are *G. hirsutum* varieties (King, 1930). There are also cultural and environmental influences. In glasshouse experiments on the effects of photosynthetic rate upon yield (Mauncy *et al.*, 1978) we observed (unpublished data) that the plants in a CO₂-enriched glasshouse had more second axillary squares than the plants in the control glasshouse. In view of the fact that, if fully expressed, this trait could produce twice as many fruiting positions in a given time, the trait appears to offer a powerful method of achieving earliness.

Unfortunately none of these second axillary sites are prime sites as defined here. The squares are at least one HFI unit later in blossoming than the first axillary flower at that node (Figure 7). Perhaps because of the competition for nutrients for growth, two bolls at a branch node is a rare event.



Figure 7. Branch on which a second axillary flower ($1F_2$) has developed. Relative timing of this position is shown by the fact that blossoming of the $1F_2$ position occurred at the same time as the second position on the first axillary ($2F_1$). The boll at the first node of the first axillary ($1F_1$) was shed from this branch.

Namken *et al.* (1978) described a genetically determined trait which causes a high percentage of plants to have one or more pairs of sympodia in an opposite configuration on the main stem rather than the typical alternate pattern. They named the trait "side-by-side". This trait shortens the VFI by an average of 0.3 to 0.5 days and significantly improves earliness.

Most reports describing efforts to breed earlier-maturing varieties have indicated that the length of time from planting to first square is well correlated with the length of time to harvesting the majority of the pickable lint. Anderson (1971b) measured a correlation coefficient of $r^2 = .45$ ($P < 0.001$) between days to 50 percent first squares and days to 85 percent of seedcotton pickable. While there was no attempt to examine the components of this earliness according to the categories of Munro, it is likely that vigor of vegetative growth, initiation of first fruiting branches at lower nodes and shortening of the VFI would contribute to this correlation.

Baker *et al.* (1973) observed that increased photosynthetic efficiency would not only increase yield but also earliness. Hearn (1969) found that varieties differed not only in the node of first sympodium but also in the HFI. He found no differences in VFI among the varieties he studied. It is apparent that several

mechanisms for earliness exist among the varieties of the world and that analysis is required to determine the components of earliness in each selection situation.

VEGETATIVE—REPRODUCTIVE RATIO

The data quantifying flower site production and interactions with environmental factors appear relatively complete. However, none seems to answer clearly the persistent question of why there are situations in which excessive square shedding or extreme vegetative growth produces tall, relatively barren plants.

The ratio of vegetative structure of each plant to the reproductive sites is a function of the number of vegetative nodes below the NFB, the vigor of vegetative limbs and the number of flower sites on each sympodium. Hearn (1969) found that plant density was a primary determinant of the number of vegetative limbs and that the number of flower sites per sympodium was determined by the genetics and internal competition among branches of each plant. Thus, in the basic sense only the number of nodes below NFB is variable for environmental and cultural control of vegetative/reproductive ratio (V/R). After floral initiation and development of the first sympodium, the morphological V/R has been fixed. In practice, however, growers observe non-productive plants and non-productive years which they attribute to cultural or weather-induced excessive vegetative growth. However, since each main stem node above NFB produces a sympodium with the potential for at least three fruiting sites, the poor V/R must be the result of excessive square shed rather than excessive vegetative growth. Without bolls to compete for carbohydrate, the vegetative main stem continues rapid proliferation of new leaves and the result is tall, unproductive, "stag" plants.

There is general belief among growers that excessive V/R tends to be self-perpetuating unless they apply cultural stresses such as delay of fertilization or irrigation schedules. Based on the growth and flowering rate relationships shown in Figure 2, I suggest the following about self-perpetuating square shed. If Figure 2 is the normal course of vegetative growth for productive plants, what is the effect of loss of the first bolls which are effective carbohydrate sinks? The rate of MSN development would remain high, and instead of the open blossoms approaching the plant apex more and more closely, they would remain 10 to 12 nodes below the apex within the canopy. Guinn (personal communication) has observed that young squares are very susceptible to shedding under conditions of shade. If, as I suggested earlier, they are primarily photosynthetically self-sufficient, the shading of the rapidly developing terminal might be sufficient to induce square shedding. To pursue this logic further, perhaps one reason that high plant populations are more likely to be "vegetative" is that self shading of squares occurs in dense stands when the plants are at an early stage of development.

Self-perpetuating square-shed may also be induced by excessive insect damage. Leigh *et al.* (1974) observed that plant bugs were a more severe problem in well-

watered, rapidly growing, closely spaced stands than in stressed and relatively open plantings.

Whatever the exact interactions which result in high V/R, the implication of the hypothesis is that the importance of setting the early bolls far outweighs their direct contribution to yield. When the first few sympodia are loaded with active carbohydrate sinks, the productive pattern represented by Figure 2 follows its natural course. Without these sinks, stem elongation, self shading, and perhaps excessive insect injury can result in tall, barren plants which are difficult to manage culturally.

GROWING-DEGREE-DAY SUMMATIONS

Because growth and maturation of the cotton plant is temperature dependent, many workers (Bilbro, 1975; Mahon and Low, 1972; Anderson, 1971a; Kerby *et al.*, 1985; Sevacharian and El-Zik, 1983) have suggested that the progress of the crop could be monitored by summations of the growing-degree-days (GDD). Fry (1983) examined the various methods of calculating average GDD summations for individual days. Most calculations seem to use 15.3C (60F) as a base temperature and no upper threshold. Kerby *et al.* (1985) suggested that use of 38C (100F) as an upper threshold would improve the correlation of GDD with growth stages.

While GDD summations can be used as a rough guideline to growth stage expectation during a season (Sevacharian and El-Zik, 1983), the summations must be qualified for cultivar, location, and year. Table 2 shows the range of values which have been assigned to aspects of crop development. Correlations would be expected to fit poorly when water or nutrient stress, insect infestations or physical damage by weather or chemicals produced an unusual plant stress.

Table 2. Range of published GDD (base 15.3C) summations for individual phases of crop growth and maturation and the seasonal sum at which these phases have been found to occur.

Growth phase	Growing degree days	
	Phase	Seasonal sum
Emergence (stand establishment)	45-130	45-130
Appearance of first square	350-450	480-530
Square period	250-500	
Appearance of first flower		740-1150
Peak blooming rate	200-800	850-1625
Boll period	910-950	
First open boll		1690-2050
Defoliation		2550-4600

SUMMARY

Because the flowering habit of cotton, *Gossypium hirsutum* L., is complex and extends over a long period of time, considerable research has been directed at describing and quantifying the production of fruiting sites by the plant. The first flower buds are borne on fruiting (sympodial) branches at the fifth to tenth main stem node. Flower buds open as blossoms about 3 weeks after they are first visible. After the first fruit (bolls) are set, the growth rate of the main stem slows, then eventually stops. For a time, blossoms open at a faster rate than new floral branches are formed. When all floral bud sites formed in the initial vegetative growth phase have matured into blossoms, there is a hiatus in flowering known as cut-out. Subsequently, the resumption of vegetative growth produces new floral sites and a second flush of flowering occurs. Though sympodia are morphologically indeterminate, they ordinarily are limited to three active floral nodes in field plantings.

All processes leading to square, blossom and boll initiation and maturation are temperature-dependent. The rate of development at 30C is three times faster than that at 18C. In favorable sunlight, temperature, moisture and nutrition environment each plant will produce about 15 to 20 sympodia and about 50 flower buds which will blossom over a period of 60 days. From these, 10 to 15 bolls can be expected to mature into harvestable lint and seed. In order to produce the same number of bolls in a shorter season the plant must begin sympodial development at a lower node, have more rapid floral organ growth, produce more flowers from a specified number of sympodial nodes or retain a higher percentage of the sites to maturity.