EFFECTS OF SHEDDING IN COTTON ON CARBOHYDRATE PARTITIONING IN ADJACENT FRUITING POSITIONS

by

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A Thesis Submitted to the Faculty of the
DEPARTMENT OF PLANT SCIENCES
In Partial Fulfillment of the Requirements
For the Degree of
MASTER OF SCIENCE
WITH A MAJOR IN AGRONOMY
AND PLANT GENETICS
In the Graduate College
THE UNIVERSITY OF ARIZONA

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ACKNOWLEDGMENTS

I wish to express the most sincere gratitude to Dr. B. Brooks Taylor for his patience and enthusiasm during the many hours of guidance he offered throughout the course of this study. More important, however, will be the lessons learned in dealing with human relationships by my association with Dr. Taylor during this period.

Appreciation is extended to Dr. Gene Guinn, Dr. Roger Huber, and Dr. Dwayne Buxton for the valuable experience gained by the opportunity to study with such quality and professional scientists.

I also thank Madonna Brooks for her many unselfish hours spent typing this manuscript.

Finally, deepest gratitude is expressed to my wife, Dawn, whose patience, encouragement, and personal sacrifice enabled me to complete this work.

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ABSTRACT

Field studies were conducted at Phoenix, Arizona to evaluate the relationships between fates of adjacent fruiting positions in cotton (Gossypium hirsutum L.).

Fruit on the first position of a sympodium (fruiting branch) abscised as a square less frequently and matured as a boll more frequently than adjacent fruit on the second position. These relationships were attributed to a greater sink strength of the first position and the proximity of the first position to a mainstem leaf.

The fates of adjacent fruiting positions were found to be dependent upon one another. Percent boll shed increased and percent fruit retention generally decreased at the second position as the fruit on the first position was maintained longer. Second position square period was not influenced by shedding at the first position. Seed cotton produced at the second position increased significantly when the first position shed.

Results indicate the second position probably serves as an alternate sink when the first position fruit sheds.

INTRODUCTION

Cotton is the world's most important fiber crop. Valuable products for human and animal consumption are also obtained from cottonseed processing. Each year in Arizona much more land is planted to cotton than any other crop.

A continuing obstacle to maximizing cotton yield is excessive shedding of fruiting forms. Evidence has accumulated that boll abscission is promoted by drought, shading, nutrient deficiencies, heavy boll load, insect feeding, and altered hormonal balance. Additional knowledge about fruiting form behavior under stress conditions is necessary in order to develop improved cultural practices, select improved varieties, and increase profits.

Research has shown that cotton bolls compete with roots and vegetative growth for plant nutrients. Further knowledge of the competition among individual fruiting forms is needed to more clearly understand some of the physiological relationships of carbohydrate levels and fruiting.

The objectives of this study were: (1) to determine the relative shedding frequencies of adjacent fruiting positions, and (2) to determine the effects of abscission at one fruiting position on development and abscission of an adjacent fruiting position.

REVIEW OF LITERATURE

Two theories of boll abscission have appeared in the literature: (1) the nutritional theory, and, (2) the hormonal theory. Both were identified by F. M. Eaton, who attributed the nutritional theory concept to T. G. Mason. Mason (1922) observed that cloudy days or leaf removal caused boll shedding, and concluded that insufficient nutrients were being produced under those conditions.

Boll Abscission Theory

The nutritional theory states that cotton plants retain only as many bolls as they can supply with the necessary nutrients. The theory is supported by the results of several studies which will be discussed later (Hawkins et al., 1933; Dunlap, 1945; Eaton and Rigler, 1945). The evidence presented therein and in other research indicates boll shedding is increased by short photoperiod, dim light, lack of available moisture, mineral nutrient deficiencies, and heavy boll load.

Eaton and co-workers conducted several experiments in an attempt to test the nutritional theory. Eaton and Ergle (1953) concluded from their results that the nutritional theory was poorly supported and suggested boll shedding is controlled by a balance between auxin and some anti-auxin produced by bolls. Eaton's "anti-auxin", now called abscisic acid (ABA), was isolated by Liu and Carns (1961). Davis and Addicott (1972) obtained evidence that ABA causes abscission. Other research with ethylene has also lent support to the hormonal theory. Lipe and Morgan (1972, 1973) presented evidence that ethylene regulates boll abscission. Both ABA and ethylene could represent the anti-auxin material.

The research results which support each theory do not refute one another. High levels of ABA and ethylene have been reported in tissues under conditions which may cause nutrient stress. In a recent chapter on boll abscission, Guinn (in press) stated, "Apparently the nutritional status of a boll affects abscission through its effects on plant hormones. Thus, the nutritional and hormonal theories for the control of boll abscission are not mutually exclusive or contradictory; nutritional and hormonal effects are just different parts of the whole control system."

The Abscission Zone and Hormonal Effects

The active processes of abscission usually occur at a morphologically distinct region at the base of the organ known as the abscission zone. Within the abscission zone, differentiation of cells is incomplete even by the time the organ is senescent (Addicott, 1970). Pectinase (Yager, 1960; Morre, 1968) and cellulase (Horton and Osborne, 1967; Abeles, 1969; Ratner et al., 1969) activities increase and weaken the peduncle prior to shedding (Morre, 1968; Webster, 1973). This weakening does not always result in fruit drop as is often seen with plants under moisture stress (Osborne, Jackson, and Milborrow, 1972). Although the fruit is aborted, squares and bolls are sometimes retained until rewatering causes growth of cells on the proximal side of the abscission zone. The growth of proximal cells and shrinkage of distal cells set up shear and tension forces which break remaining vascular connections (Morre, 1968; Leopold, 1971).

Hormonal balance, particularly at the abscission zone, controls abscission. Exogenous applications of auxins to abscission zone explants can stimulate or inhibit abscission depending upon location and timing of application (Guar and Leopold, 1955; Louie and Addicott, 1970). The stimulation of abscission by auxin may be explained by its ability to promote ethylene production (Morgan and Hall, 1962, 1964), and by a sensitivity of tissue to ethylene induced by excission (Leopold, 1971). Auxin application to intact plants generally, but not always, retards abscission (Addicott, 1970). Auxin may inhibit abscission by preventing the aforementioned increase in cellulase activity (Abeles, 1969; Ratner _et_ _al_., 1969; Lewis and Varner, 1970), or as suggested by Guinn (in press), by its ability to maintain membrane integrity and, thereby, prevent secretion of pectinase and cellulase through the plasma membrane. Auxin also inhibits abscission by mobilizing nutrients towards fruits and leaves (Addicott, 1970).

Ethylene is capable of strongly accelerating abscission of a variety of plant parts and organs (Burg, 1968). Morgan and coworkers have done a great deal of work with auxin, ethylene, and auxin-ethylene interactions. Besides showing that auxin promotes ethylene production, they have obtained evidence that ethylene increases IAA oxidase activity (Morgan and Hall, 1962; Hall and Morgan, 1964; Morgan et al., 1968) and decreases auxin transport (Morgan et al., 1968; Beyer and Morgan, 1969, 1970, 1971). Morgan and Durham (1975) showed that slowed auxin transport stimulates abscission. Ethylene has also been shown to increase cellulase synthesis (Horton and Osborne, 1967; Abeles, 1969; Ratner et al., 1969). Abeles et al. (1971) demonstrated that ethylene aids the secretion of cellulase through the plasma membrane. Ethylene, therefore stimulates abscission by: (1) increased auxin destruction and slowed auxin movement, and (2) increased cellulase synthesis and secretion to abscission zone cell walls.

Many effects of ethylene and ABA are similar. Addicott (1970) suggested that ABA serves as a "non-volatile ethylene" in the control of abscission. Davis and Addicott (1972) showed ABA content was high when abscission was high. ABA probably has both direct and indirect effects on abscission. ABA can cause increased ethylene production in some plants (Craker and Abeles, 1969; Abeles et al., 1971) and increased cellulase activity (Craker and Abeles, 1969).

Gibberellins (GA) and cytokinins (CK) appear to inhibit shedding of intact fruit by mobilizing nutrients to the fruit (Addicott, 1970). Results of studies by Walhood (1957) and Johnson and Addicott (1967) support the hypothesis that GA increases the competitive ability of cotton squares and bolls to accumulate nutrients. Cytokinins also have been shown to increase the ability of an organ to compete for assimilates (Letham, 1967). However, exogenous applications of cytokinins have both promoted and inhibited abscission according to Varma (1976a, b). Applications of cytokinin promoted abscission unless application was made directly to the abscission zone.

The possibility of another endogenous agent which promotes abscission, a senescence factor (SF), has been investigated by some workers. Most of this work, however, has utilized leaf blade and petiole explants. Osborne et al. (1972) obtained a material from senescent petioles which stimulated ethylene evolution by and abscission of explants. Guinn (1977) extracted a heat-stable material from cotton bolls, after destroying membranes by freezing, which stimulated ethylene evolution by healthy bolls. It is not known whether these and other scientists identifying a SF have been working with the same substance.

Environmental and Cultural Effects

An actively growing plant is a highly sensitive organism, responsive to very small changes in the environment. This is particularly evident in relation to abscission. Plants have evolved a set of physiological mechanisms that can come into action rapidly and help to maintain a functional homeostasis under adverse conditions. Conversely, in the presence of unusually favorable conditions, the plant will delay abscission appropriately. The list of climatic, edaphic, and other factors potentially affecting abscission is long. Only those factors known to influence abscission in cotton will be discussed here.

Light

Light has a great influence on many aspects of plant growth and development, primarily through its effect on photosynthesis. The term photosynthetic irradiance (PI), radiant energy flux density of photosynthetically active radiation (400 to 700 nm), has recently been accepted for use in relation to photosynthesis (Shibles, 1976). The term irradiance, therefore, will be used in this paper instead of the oft used light intensity.

The effects of irradiance upon cotton fruiting and shedding have been studied for many years. In investigations with Sea Island cotton, Mason (1922) cited cloudy days and daytime rain as conditions retarding boll growth and augmenting boll shedding. Dunlap (1945) reported low irradiance and short days were more important factors of shedding than high temperatures or low available moisture. Goodman (1955) also correlated cloud shade with increased shedding and noted some varieties were more susceptible than others. Rain accompanying cloudy weather may also increase shedding by rupturing pollen in open flowers (King, Tang, *et al.*, 1956).

F.M. Eaton and co-workers conducted a series of experiments in which the effects of irradiance upon carbohydrate levels and fruiting activities were investigated. Eaton and Rigler (1945) and Eaton and Ergle (1953) observed increased square shedding in plants grown under low irradiance. Eaton and Ergle (1953) noted the carbohydrate content of 13-day-old bolls was least when plants were shedding most heavily. Decreasing irradiance by 68% of full sunlight decreased starch plus sugar content of stems, leaves and bolls and decreased yield by more than 50% (Eaton and Ergle, 1954). When half of each leaf was removed the number of bolls per plant and yield were decreased 24 and 14%, respectively.

Square and boll abscission is affected by leaf area and leaf shape. Johnson and Addicott (1967) varied leaf area by cutting away half of each leaf and by removing alternate leaves. Both treatments decreased boll retention and yield, and achieved similar ratios of total leaf area to bolls retained. The authors obtained evidence that bolls retained later in the season contained more seed per boll. They made the interesting suggestion that, because there was increased competition for assimilates late in the season, boll retention may be dependent on the presence of more seed to mobilize assimilates. Cotton cultivars with normal, okra, and superokra leaf types tend to have high, medium, and low leaf area indices (LAI, ratio of leaf area to land area) respectively. Kerby and Buxton (1976) found that okra and superokra plants produce more fruiting positions than normal leaf cultivars but also shed more squares. They suggested that a decrease in the production of carbohydrates per fruiting position may be a factor in the higher shedding cultivars.

Guinn (in press) indicated that irradiance probably affects abscission because of its effect on photosynthesis and carbohydrate supply, and he demonstrated that factors which increase photosynthesis and decrease respiration increase boll retention and yield (Guinn 1974a, Guinn _et al._, 1976). In a recent study by Kittock and Fry (1977), Pima (_Gossypium barbadense_) plants with tops removed produced many more bolls on branches near the cutting than on branches at the same position on plants without top removal. They suggested that topping allowed greater irradiance and, therefore, increased carbohydrate production by treated branches.

Guinn (1976a) and Vaughan and Bate (1977) have shown a nutritional stress, incurred by low-irradiance, long warm nights, or heavy boll load, increases ethylene evolution by young bolls. Both studies negatively correlated sugar content and ethylene evolution. ABA levels in bolls also increased when plants were placed under low irradiance (Guinn, 1974b) or darkness (Vaughan and Bate, 1977). Thus, low irradiance may cause an increase in production of two abscission promoting hormones.

Temperature

Temperature has profound effects on many metabolic processes directly and can have indirect effects through changes in composition and transport of materials from plant organs. The physiological processes of abscission have been shown to be maximized at 30 C for beans (*Phaseolus vulgaris*) and at 35 C for cotton in abscission zone explants (Addicott and Lyon, 1973).

Powell (1969) observed cotton plants under various temperature regimes in controlled environments. Continuous high temperatures caused malformed flowers with little or no pollen. A short period of reduced temperature in the 24-hour cycle increased boll retention. High-temperature-induced square and boll abscission has been reported often (Dunlap, 1945; Powell, 1969; Bhatt *et al.*, 1972; and Guinn, 1974a). However, Ehlig and LeMert (1973) concluded that fruit load was primarily responsible for boll shedding and they could not correlate boll retention with temperature fluctuations. Patterson *et al.* (1978) also associated increasing boll load with increasing shedding.

High temperatures have been shown to increase dark respiration and photorespiration (Laing *et al.*, 1974; Ku and Edwards, 1977). Increased respiration leads to decreased net photosynthesis, and thereby reduced translocatable assimilates (Baker, 1975). A variation in sensitivity of these processes in cotton plants may help explain the apparent difference in heat tolerance of some cotton cultivars (Feaster and Turcotte, 1965; Fisher, 1975).

Low temperatures may cause a reduction in photosynthesis (Taylor and Rowley, 1971) and reduced protein synthesis and amino acid accumulation (Taylor *et al.*, 1972). Boll retention, however, appears to be relatively unaffected by low temperature (Dunlap, 1945; Gipson and Joham, 1968).

Water

Lack of available moisture has long been accepted as a cause of shedding in cotton (Ewing, 1918; Lloyd, 1920; Hawkins *et al.*, 1933). This response may be a survival mechanism freeing assimilates for increased root growth.

Growing crops acquire water primarily by two methods: (1) capillary movement of soil water to roots; and (2) the growth of roots into moist soil (Buckman and Brady, 1969). Capillary movement through drying soil is greatly reduced (Richards and Richards, 1957). Therefore, to obtain water the roots must extend to moisture. Quisenberry and Roark (1976) concluded that less determinate cotton cultivars are better adapted to limited moisture environments (dry land farming). Guinn (in press) suggests this is due to the less determinate cultivar's ability to put on more root growth because a smaller boll load is competing for assimilates.

McNamara, Hooton and Porter (1940) observed young bolls shed most frequently while older bolls were virtually always retained. Eaton and Joham (1944) reported that defruiting caused increases in sugar content and root growth. Under moisture stress, shedding may be a response which utilizes the reduced nutrient supply for root growth into moist soil and maintenance of older bolls.

Irrigation timing and quantity have been shown to influence plant growth, fruiting, and shedding. Allowing plants to stress during flowering is most detrimental to crop yield (Longenecker and Erie, 1968; Grimes _et al_., 1970). A preflowering stress may induce increased fruiting rate (Singh, 1975). Stockton _et al_., (1961) reported increasing plant height, flower production, and shedding with increasing frequency of irrigations. Intermediate treatments retained as many bolls as treatments with twice as many irrigations. Similar results have been obtained by Hawkins _et al_., (1933). However, Crowther (1934) reported low shedding with medium irrigation but highest yields with frequent irrigation.

Water deficits can affect many physiological processes which may influence abscission. Moisture stress decreases leaf area, photophosphorylation, polyribosome content, and protein synthesis, and causes stomates to close (Boyer, 1973, 1976). Water deficit has also been shown to decrease synthesis and activity of ribulose 1,5-biphosphate carboxylase (Jones, 1973) and increase photorespiration

(Lawlor and Fock, 1975). Many of these effects may decrease net photosynthesis and, thereby, create a nutrient shortage.

Hormonal balance is also upset by a moisture deficit. Itai and Vaadia (1965) found cytokinin levels decreased when sunflower plants were stressed to wilting. ABA content (Jordon _et al_., 1975; Zeevaart, 1971; Milborrow, 1974) and ethylene production (McMichael _et al_., 1972; Guinn, 1976b) increase with a decrease in available moisture. ABA was shown to enhance boll abscission and ABA levels in bolls were found to be higher in a higher shedding cultivar (Davis and Addicott, 1972). Guinn (1976b) reported increasing ethylene production by bolls as they desiccated, but the ABA content of bolls of droughted plants has not been reported. Lack of available moisture, as well as low irradiance, may therefore cause an increase in two abscission promoting hormones.

Water-logged conditions from over-irrigation, low infiltration rates, or flooding can be as detrimental to yield as excessive moisture deficits. Percolating water leaches out nutrients and can drastically reduce root aeration (Buckman and Brady, 1969). Both conditions can cause shedding (Longenecker and Erie, 1968). Waterlogging stimulates ethylene production in soil and the ethylene moves up the plant. In the short term, this is probably more important than leaching (G. Guinn, personal communication).

Inorganic Nutrients

Abscission of leaves, buds, flowers, and fruit is a common response to mineral deficiency (Kozlowski, 1973). Deficiencies of

N,P,K,S,Ca,Mg,Zn,B, and Fe have been associated with abscission (Sprague, 1964; Treshow, 1970; Addicott and Lyon, 1973). Nitrogen is the most heavily used fertilizer in cotton production and is present in virtually all plant parts — the amino acids serving as a pool of intermediates for many more specialized compounds. A nitrogen deficiency can cause shedding (Addicott and Lynch, 1955; Tucker and Tucker, 1968) and may be a major factor in cut-out of cotton (Guinn, in press). Available N was considered a factor controlling abscission of squares, bolls, and leaves in a cotton growth model developed by J.D. Hesketh and co-workers (Jones _et al._, 1974; Thompson _et al._, 1976).

Nitrogen supply affects rate and duration of flowering (Tucker and Tucker, 1968) as well as boll retention. High rates of N application have been shown to cause high shedding but also high yields (Crowther, 1934; Reddy and Rao, 1970). Eaton and Ergle (1953) attempted to influence fruiting and shedding by foliar N applications. N levels increased but boll shedding also increased.

The level of auxin, an abscission inhibitor, has been correlated with soil N (Averly _et al._, 1937). According to Addicott and Lyon (1973), Carns, Hacskaylo, and Embry (1955) obtained evidence that decreasing soil N predisposes plants to chemical defoliation. Nitrogen deficiency may also increase ABA content (Goldbach _et al._, 1975). These effects may be the result of a decreased nutrient supply due to low N supply limiting photosynthesis (Nevins and Loomis, 1970).

Boron (Eaton, 1932; Lancaster *et al.*, 1962; Hinkle and Brown, 1968) and calcium (Joham, 1957; Addicott and Lynch, 1955; Addicott and Lyon, 1973) deficiencies are accepted as causing square and boll abscission. Both are required for the maintenance of healthy phloem (Guinn, in press) and there is evidence both promote translocation (Eaton, 1955; Joham, 1957). Guinn (in press) suggests K and Zn may also affect shedding because deficits of these minerals may cause decreased photosynthesis or hormone imbalance.

Assimilate Partitioning

Several studies have associated decreased boll retention and flowering with decreased assimilate supply; Mason (1922); Eaton and Ergle (1953, 1954); Johnson and Addicott (1967); Ehlig and LeMert (1973). Developing bolls represent strong sinks and boll shedding generally increases from beginning to end of the season. Verhalen *et al.* (1975) reported boll retention rates decreased from near 80% early in the season to less than 10% by the end of the season. Ehlig and LeMert (1973) obtained a high negative correlation between the percent daily boll retention and cumulative boll retention. They concluded that heavy boll load was the primary cause of midseason cut-out (reduced growth and flowering rate). Similar results were obtained by Patterson *et al.* (1978). They found percent boll set and number of flowerings developing into mature bolls were high during the normal cut-out period when boll load was restricted. Eaton (1931a) reported early season debudding resulted in increased yield because of increased total boll set by the season. Results from similar studies have not consistently shown yield increases (Hamner, 1941; Dunman, Clark, and Calhoun, 1943; Patterson *et al.*, 1978). The evidence indicates boll abscission may be associated with increased demand as well as decreased supply of carbohydrates.

Hearn (1972) postulated that bolls are retained only if the demand does not exceed the supply. He defined boll demand using daily growth rate per boll and total number of bolls per plant. His results indicated boll demand increased to a maximum at which time bolls began to shed heavily. In further support of his hypothesis, he developed a model to predict yield that accounted for nonrandom yield variation between cultivars and planting dates. The correlation between yield and various crop parameters increased greatly when boll demand equalled or exceeded crop growth rate.

Saleem and Buxton (1976) showed that vegetative and reproductive growth compete for available carbohydrates and that heavy boll load reduces the stem carbohydrate level. Bolls also compete with roots for assimilates and can inhibit root growth (Eaton, 1931b; Crowther, 1934). Eaton and Joham (1944) reported that defruiting caused increased root sugar content and root growth. This may help explain part of the variation in abscission rates of different cultivars (Verhalen *et al.*, 1975; Patterson *et al.*, 1978). More determinate cultivars are more responsive to controlled boll set (i.e., debudding causes a greater increase in percent boll retention), possibly because development of an early boll load is a more important factor in fruiting habit of these cultivars versus less determinate cultivars (Patterson et al., 1978).

Bolls also may compete with one another for plant carbohydrates. Loomis (1927) reported on observations made during a study in 1924 and 1925 in Arizona. He noted that boll retention was highest at the first fruiting position of a sympodium and decreased out the branch. In 1925, he reported 55.1, 60.9, 79.6, and 84.6 percent of bolls shed at the first, second, third, and fourth node, respectively. Likewise, of squares initiated on the same date, square period and boll maturation period increased from the first to fourth fruiting positions. He claimed the presence of a boll at the first position appeared to lengthen the boll period at the second position but no data were presented. Boll period on all nodes lengthened as the season progressed. Loomis (1927) suggested higher population cotton culture could produce higher yields by preventing growth of long fruiting branches which shed more bolls.

High plant populations should, in theory, produce an earlier crop, by increasing solar radiation interception early in the season (until the canopy closes). However, anticipated results have not always been observed due to low fruiting and high shedding rates (Brown, 1971; Gerard et al., 1976a,-b). The most likely cause of poor fruiting of crowded plants is low irradiance in the canopy (Guinn, in press). Crowding can decrease boll size (Bridge et al., 1973; Hawkins and Peacock, 1973), which may also be the result of shading.

The leaf subtending a boll is the most important source of photosynthate for that boll (Ashley, 1972; Brown, 1973; Benedict and Kohel, 1975; Horrocks et al., 1978). Horrocks et al. (1978) showed that at least three leaves are important in supplying assimilates to a boll located at the first position on a sympodial branch. Primary sympodial bolls received 41% of their C^{14} assimilate from the subtending leaf, 38% from the second sympodial leaf, and 21.5% from the main stem leaf. Similar results have been observed in groundnut (Arachis hypogaea L.) (Khan and Akosu, 1971), rape (Brassica campestris L. 'span') (Major and Charnetski, 1976), and soybeans (Glycine max L.) (Thrower, 1962) which suggest sink strength is inversely proportional to the distance from source.

King, Tang et al., (1956) found that bolls could be forced to develop from unfertilized ovaries if sympodia with one boll were girdled to prevent translocation of assimilates out of the branch. Sucrose applications delayed shedding of bolls from shaded branches (King, Ni et al., 1956). On sympodia with a heavy boll load, most assimilate produced within that branch remain within that branch (Ashley, 1972; Brown, 1973). Shedding of first position bolls may increase retention at the second position of a sympodium (T. Kerby, unpublished data). These results indicate that supply and demand of photosynthate are important factors in controlling boll set on individual sympodia.

MATERIALS AND METHODS

Field studies were conducted on Avondale clay loam, a member of the fine, loamy, mixed Hyperthermic Torrifluventic Haplustolls, during 1976 and 1977 at the Cotton Research Center (CRC) in Phoenix. "Deltapine 61" was planted on 31 March 1976 and 5 April 1977 in irrigated rows 102 cm apart. Standard cultural practices were used for fertilization, irrigation, weed control, and late season insect control. This study was part of a larger study on early season fruiting habits and insect control. Experimental design of the larger study was a randomized complete block with five replications of five early season insect control regimes.

Plant mapping observation plots in each replication were thinned to 10 plants in 152 cm of row and 20 plants in 305 cm of row in 1976 and 1977, respectively. No significant differences between insect control treatments were observed in the plant mapping data, therefore, data was pooled for analysis. Each plant was observed 2-3 times weekly beginning 24 and 31 May and ending 17 and 23 August in 1976 and 1977, respectively.

The dates were recorded for each leaf unroll, square seen, white bloom, and for square or boll abscission. The mainstem node position of each branch (vegetative or fruiting) and nodal position of each fruit were also recorded. Square seen dates were recorded when the bract reached 5-6 mm wide. Bloom dates which did not occur on an observation day were estimated by interpolation in the field. Abscission dates were recorded as the median of the before and after abscission observation dates.

Mapping data were entered into a computer to facilitate analysis. All programs contained routines to eliminate widely dissimilar plants and unrealistic data. Data from both years were handled in a similar manner.

Leaf unroll dates of mainstem and fruiting branch leaves were used to calculate fruiting nodes formed.M^{-2}.day^{-1}. First and second fruiting position shedding data were obtained from sympodia having at least two nodes. Contingency tables were compiled from the shedding data to determine the independence of the fate of the two positions. Square periods were calculated from the square seen to bloom dates of each square.

Temperature data were obtained from CRC records.

Three 25-boll samples were collected from each replication of the insect control check on 22 September 1977 as follows:

1) First position bolls from sympodia with a second position boll.
2) Second position bolls from sympodia with a first position boll.
3) Second position bolls from sympodia without a first position boll.

Samples were weighed and ginned to determine seed cotton weight and number of seed per boll. Fiber was analyzed for length, strength, and fineness (micronaire) at the University of Arizona Cotton Fiber Lab.

RESULTS AND DISCUSSION

Weekly averages of fruiting positions formed.M^{-2}.day^{-1} for 1976 and 1977 are shown in Fig. 1. Fruiting rate followed a similar pattern both years (r=0.92), reaching a peak in early July and then declining, although more fruiting positions were formed in 1977 than in 1976. Patterson *et al*. (1978) reported similar observations in cotton grown in Arizona in 1962 and 1964. Buie (1929) found that 23 of 24 cotton varieties reached peak fruiting during the fourth or fifth week of fruiting. The curves in Fig. 1 represent the first, and economically most important, fruiting cycle of the cotton plant.

The data of Patterson *et al*. (1978) show flower production began to increase again in September of 1962 and late August of 1964. Current production practices attempt to maximize yield by maintaining the crop into the second fruiting cycle. However, increasing production costs, particularly for water and late season insect control in the arid Southwestern USA, have caused some to suggest early chemical termination of the crop (Adkisson, 1972; Kittock *et al*., 1973; Kittock and Arle, 1977).

Although varieties adapted to short season production may be developed, early season pests, such as the lygus bug (*Lygus hespersus* Knight), may become increasingly important considerations under short season culture systems. Plants would have less time before defoliation to set fruit in compensation for shedding caused by lygus and other pests.

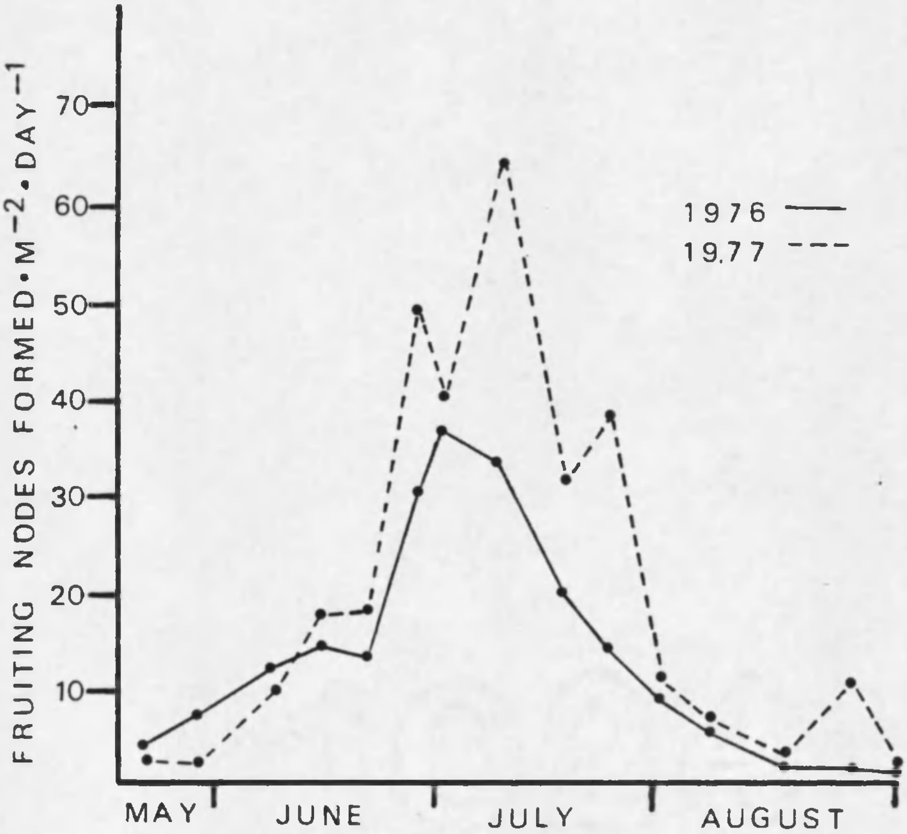

Fig. 1. Seasonal fruiting habit of cotton grown at Phoenix during 1976 and 1977.

First and Second Position Shedding

Percent square shed, boll shed, and boll retention at the first and second positions on a sympodium for 1976 and 1977 are given in Table 1. Early season (mainstem nodes 11-15) square shed was high for both positions in 1976, but not in 1977. The early boll set in 1977 compared to 1976 may be associated with an earlier cut-out.

Ehlig and LeMert (1973) and Patterson _et al_. (1978) have shown that boll load is related to cut-out (reduced vegetative growth and flowering) in cotton. Several observations in Table 1 are consistent with this hypothesis. The number of sympodia decreased as the season progressed both years. The decrease represents an increase in the number of sympodia which had developed less than two fruiting positions at the end of the sampling period, i.e., reduced reproductive growth. Boll retention at the first and second positions reached a maximum on sympodia from mainstem nodes 16-20 in 1976, but reached a maximum at nodes 11-15 and then declined in 1977. Ehlig and LeMert (1973) and Patterson _et al_. (1978) were able to increase both flower production and boll retention by defloration treatments. The high early boll set in 1977 probably caused the high square shed and low boll retention later in that season (mainstem nodes 21-25).

Although the number of sympodia was similar late in both years (nodes 21-25), the late season decrease in the number of

Table 1. Percent square shed (SS), boll shed (SB), boll retention (B) at the first and second position on a sympodium, and total number of sympodia considered. -- Values are grouped into four mainstem node segments for cotton grown in 1976 and 1977.

Sympodial Node	Mainstem Node											
	11-15			16-20			21-25			11-25		
	SS	SB	B	SS	SB	B	SS	SB	B	SS	SB	B
						1976						
First	42	16	42	23	23	54	18	34	48	29	23	48
Second	52	20	28	39	25	35	47	32	21	47	25	29
No. of Sympodia		1030			895			742			2667	
						1977						
First	17	20	63	11	40	49	28	51	21	16	33	51
Second	26	33	41	48	39	13	79	16	5	43	32	25
No. of Sympodia		1819			1545			674			4037	

sympodia considered was much greater in 1977 than in 1976. Again, the early boll load in 1977 may have been responsible by causing plants to cut-out sooner that year. Boll abscission increased at both positions during 1976, and except at the second position on sympodia from mainstem nodes 21-25, during 1977. It is not unusual to find a sharp decline in boll abscission late in the season (G. Guinn, pers. comm.). As the plants approach cut-out a large percentage of the fruiting positions abscise as squares and more assimilates become available as older bolls approach maturity. Because there are few young bolls present at that time (most positions having shed as squares), those present have a higher probability of being retained. The level of boll retention and number of sympodia indicate plants in 1977 approached cut-out sooner than plants in 1976. The decrease in boll abscission at the second position (mainstem nodes 21-25) may indicate the beginning of renewed growth and resultant increase in assimilate supply.

Heavy boll load may cause increased abscission and decreased flowering rate in several ways: a) Older bolls are stronger sinks than squares and young bolls, and, therefore are better able to compete for available nutrients. b) Root development is inhibited by competition for carbohydrates and other nutrients by developing bolls (Eaton, 1931a; Crowther, 1934; Eaton and Joham, 1944). Roots under a nutrient stress may decrease growth and water and ion uptake. c) Hormonal balance may be upset. Davis and Addicott (1972) measured ABA in bolls early and late in the season. Bolls retained late in the season had lower ABA concentrations than bolls abscissed. Guinn (1976a) showed that ethylene production increased in young bolls subjected to a nutritional stress.

Square shedding was lower and boll retention higher at the first than the second fruiting position during both seasons (Table 1). This observation is consistent with those of Loomis (1927) and Kerby (unpub. data). Loomis reported that square shed increased and boll retention decreased at successive nodes from the first to the end of the sympodial branch, but he attempted no explanation. The results of this and other research suggest that the fruit at more basal positions of a sympodium are probably more competitive for nutrients than the fruit at more distal positions.

Horrocks _et al_. (1978) have shown that the leaf subtending the first position boll, the leaf subtending the second position boll, and the mainstem leaf subtending the sympodium are important in supplying assimilates to the first position boll. Saleem and Buxton (1976) reported that total available carbohydrate levels of the mainstem were lowest at that position, where most developing bolls were located. First position fruit are closer to the mainstem and mainstem leaf, two potential nutrient sources, than second position fruit. Thrower (1962) has obtained evidence in soybean (_Glycine max_) that translocation to the fruit (pods) is inversely proportional to the distance from the source.

The first position fruit is also generally older than the second position fruit. Sympodia grow at a rate of approximately one node every 6 days (Ray and Richmond, 1966). Benedict et al. (1973) obtained evidence that a boll is at peak sink strength at about 10 days old. Young bolls are much more likely to shed than older squares or bolls. Therefore, the first position would be near maximum sink strength when the second position boll is most susceptible to shed. Thus, the first position fruit is probably more competitive for assimilates than second position fruit by virtue of its morphological location and physiological age (sink strength).

Tables 2 and 3 are sets of contingency tables relating shedding (or retention) at the second position to shedding (or retention) at the first position for 1976 and 1977, respectively. Values are percentages of second position fruit which shed as a square, shed as a boll, or matured dependent upon the fate of the first position. Chi square values indicate a significant dependence of the fate of each position upon the fate of the adjacent position at the 0.01 level.

Because age of fruit on adjacent sympodial positions differ by about 6 days, a young boll at the first position would be competing with an old square at the second position. Because young bolls are not very competitive and old squares do not shed readily, little effect of the presence of a first position fruit on square shedding at the second position could be expected. However, shedding or retention at the first position on a fruiting branch might be expected to influence boll shedding or boll retention at the second position on that branch, particularly during normal growth. The data appear

Table 2. Relationship between shedding at the second position on a sympodium and the fate of the first position on the same sympodium for cotton grown in 1976. -- Values represent shedding percentages (square shed (SS), boll shed (SB), boll retention (B)) of the second position based upon the fate of the first position (SS, SB, B). Values are from sympodia grouped into four mainstem node segments.

Condition		Percent Second Position Shed						
		Mainstem Nodes 11-15				Mainstem Nodes 16-20		
		SS	SB	B		SS	SB	B
Fate of First Position	SS	60	14	26	SS	42	15	43
	SB	48	20	32	SB	42	23	35
	B	46	25	29	B	37	31	32
		$X^2 = 23.00^{**}$				$X^2 = 20.57^{**}$		
		Mainstem Nodes 21-25				Mainstem Nodes 11-25		
		SS	SB	B		SS	SB	B
Fate of First Position	SS	53	21	26	SS	54	15	31
	SB	51	27	22	SB	47	24	29
	B	42	39	19	B	42	31	27
		$X^2 = 17.84^{**}$				$X^2 = 63.86^{**}$		

[**] Chi square values significant at the $p \leq 0.01$ level; $\sigma = 13.28$

Table 3. Relationship between shedding at the second position on a sympodium and the fate of the first position on the same sympodium for cotton grown in 1977. -- Values represent shedding percentages (square shed (SS), boll shed (SB), boll retention (B)) of the second position based upon the fate of the first position (SS, SB, B). Values are from sympodia grouped into four mainstem node segments.

Condition		Percent Second Position Shed						
		Mainstem Nodes 11-15				Mainstem Nodes 16-20		
		SS	SB	B		SS	SB	B
Fate of First Position	SS	30	18	52	SS	54	27	19
	SB	29	22	49	SB	60	28	12
	B	24	40	36	B	37	51	12
		$X^2 = 76.88^{**}$				$X^2 = 97.00^{**}$		

		Mainstem Nodes 21-25				Mainstem Nodes 11-25		
		SS	SB	B		SS	SB	B
Fate of First Position	SS	88	8	4	SS	53	17	30
	SB	79	15	6	SB	57	73	20
	B	66	30	4	B	32	43	25
		$X^2 = 634.40^{**}$				$X^2 = 301.09^{**}$		

** Chi square values significant at the $p \leq 0.01$ level; $\sigma = 13.28$.

consistent with this hypothesis. It is much easier to see trends in second position boll shedding than square shedding. If plants are stressed, the physiological response of shedding fruit may well be much stronger than any competition effects between positions.

Second position boll shedding (SB) increased as the first position fruit was maintained longer (SS to SB to B) for all mainstem node segments analyzed in 1976 and 1977 (Tables 2 and 3). T. Kerby (unpub. data) reported similar observations on cotton with three different leaf types grown in 1973 and 1974. Kerby's data show second position boll shedding increases of approximately 60% while the current data show increases of about 100%. This response could be expected if the supply of nutrients were insufficient to maintain both the 1st and 2nd positions. The second position probably serves as an alternative sink when the first position abscises.

More bolls were retained at the second position if the first position shed as a square than when the first position shed as a boll or was maintained to maturity when considering the combined mainstem segments (mainstem nodes 11-25, Tables 2 and 3), of both seasons. The second position bolls retained in this case utilize nutrients which otherwise would have gone to the first position square or boll. A strong tendency for second position boll retention (B), to decrease as the first position was retained longer (SS to SB to B) was not observed, possibly because these competitive effects on abscission were subordinate to other environmental and internal factors causing shedding at both positions.

Second position shedding (SS, SB) appeared to have little influence on abscission or retention at the first position (Tables A-1 and A-2). However, the first position consistently set more bolls when the second position shed as a boll. This observation again suggests that the presence of a first position boll increases boll shedding (SB) at the adjacent position.

First and Second Position Square Period

Square period of the first and second position decreased during 1976 and 1977 (Figs. 2 and 3). Significant correlations were obtained between square period and the corresponding mainstem node of that square. This observation is in direct contrast to that of Loomis (1927), who reported both square and boll period increased as the season progressed.

The cause for the decreasing square period is not clear. Possible explanations are suggested: the rate of development of the square may have increased by increasing daily mean temperature (Fig. 4). Hesketh *et al*. (1972) obtained evidence from two studies that square period decreases with increasing temperature. Moraghan *et al*. (1968) found variation among diverse cotton strains in both temperature and day length effects on the time of squaring but did not report on square period. Although daily mean temperature did not increase through the entire observation period and appeared to level off after the first of July, as the plant approaches cut-out, internodes shorten and squares occur on a more favorable position on the plant relative to light and temperature. Thus, higher

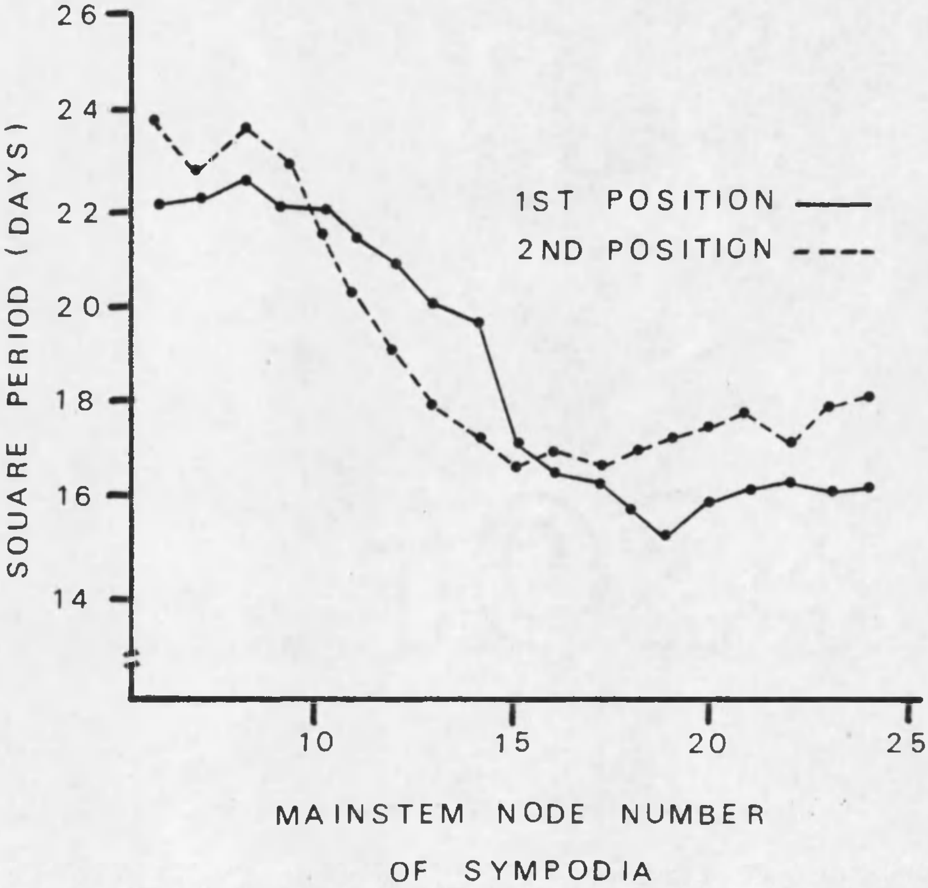

Fig. 2. Square period of the first and second fruiting branch positions for cotton grown at Phoenix during 1976.

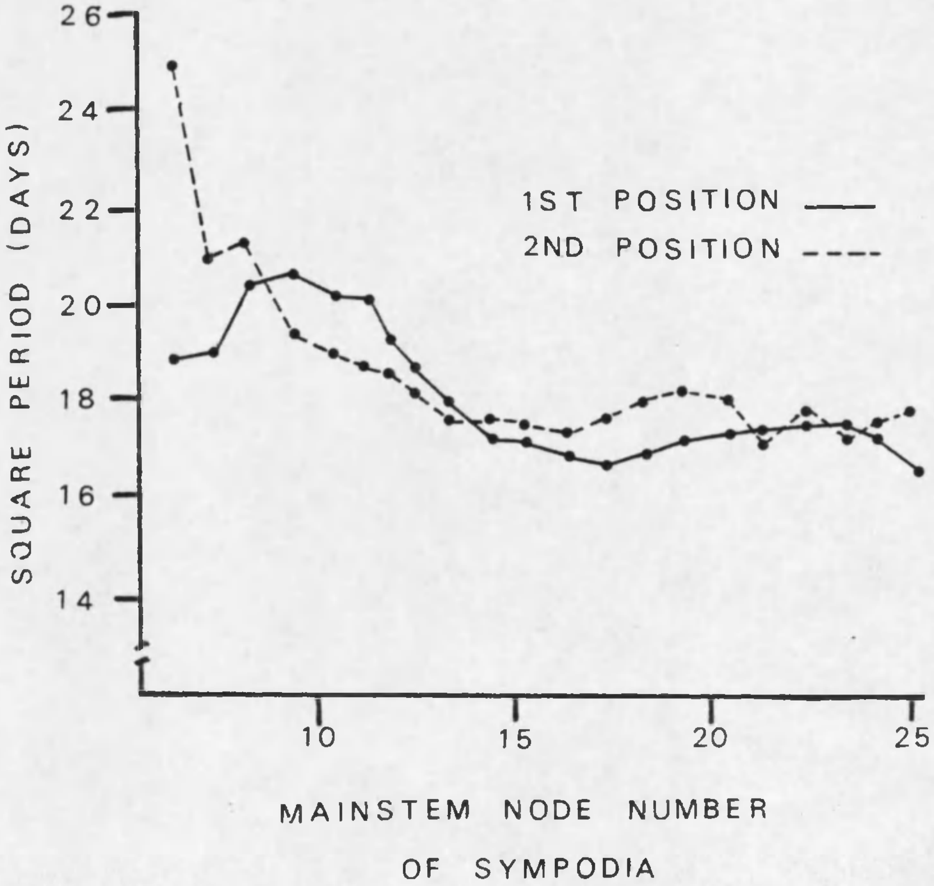

Fig. 3. Square period of the first and second fruiting branch positions for cotton grown at Phoenix during 1977.

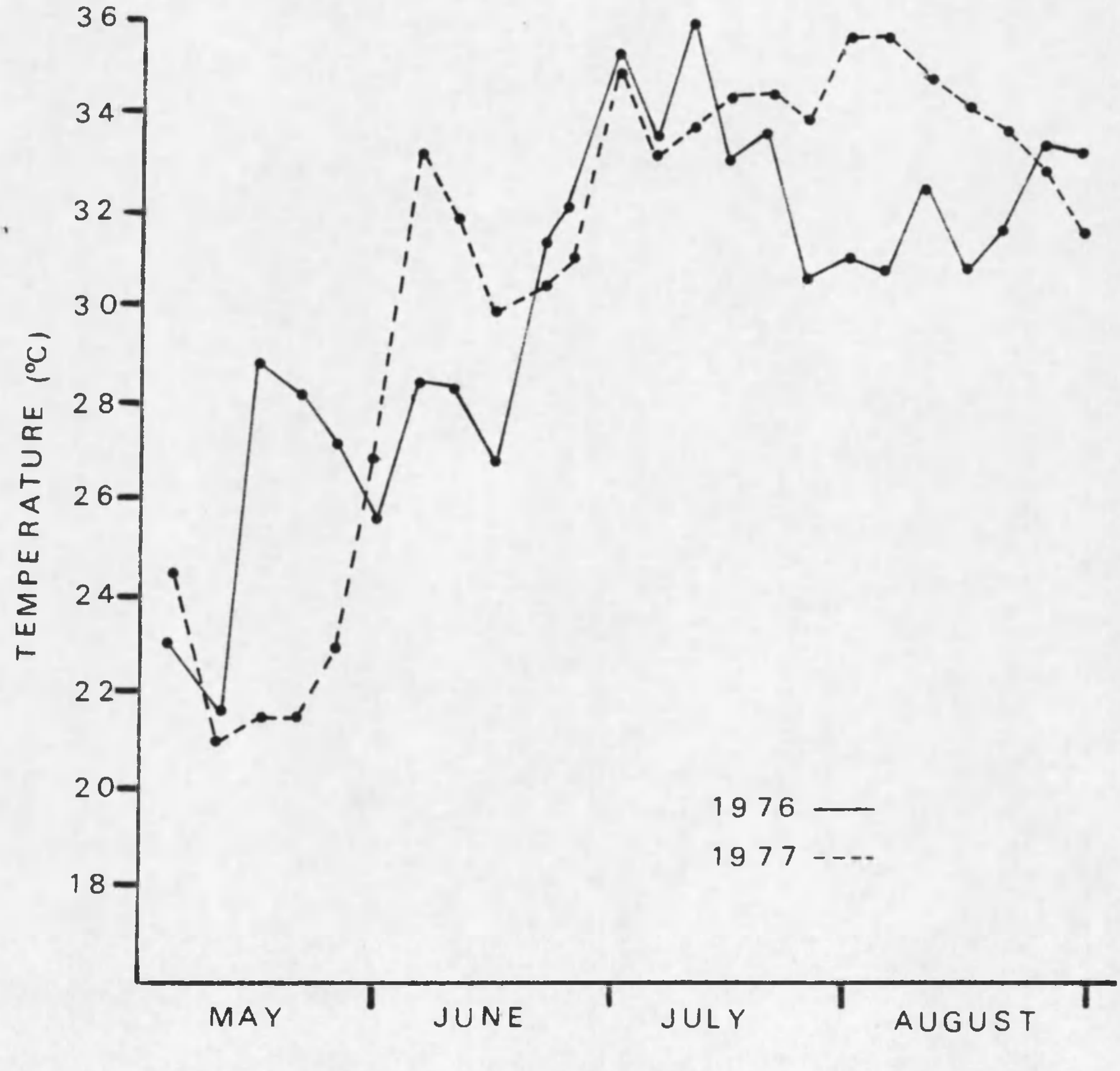

Fig. 4. Daily mean temperatures recorded at Phoenix during 1976 and 1977.

irradiance and temperature may have caused a more rapid development of the squares.

Shedding at the first position appeared to have no effect on the square period of the second position (Table A-3). This response could be expected as previously discussed.

Competition Effect on Seed Cotton and Fiber Properties

Seed cotton weight (25 boll samples) of first and second position bolls are shown in Table 4. If the first position boll was retained, it contained more seed cotton than the second position boll. Shedding at the first position of a fruiting branch caused significant increases in seed cotton weight of the second position bolls. The second position apparently benefits from the loss of a sink at the first position.

Second position bolls attained weights similar to those of first position bolls when the first position shed and did not gain weight equal to that of first position bolls. Probably only a portion of the assimilates made available by abscission at the first position are partitioned to the second position.

Similar non-significant increases were observed in second position seed/boll, % lint, fiber strength, and micronaire (fiber fineness) (Table A-4). These results provide further evidence that individual adjacent fruit on a sympodium compete for nutrients. More subtle effects may occur in fruit further from the position which sheds. No changes were observed in fiber length indicating that characteristic is probably strongly genetically controlled.

Table 4. Effect of shedding at the first position of a sympodium on the seed cotton weight (25-boll samples) of second position bolls during 1977.*

Sympodial Position	Seed Cotton Weight (grams)
First	105.28 a
Second w/ first position shed	99.03 a
Second w/ first position present	89.78 b

*Means followed by the same letter do not differ by the Duncan Multiple Range Test at the 0.01 level.

SUMMARY AND CONCLUSION

Field studies were conducted with Gossypium hirsutum L. cultivar 'Deltapine 61' at Phoenix during 1976 and 1977 to determine the effects of shedding at one fruiting position on growth and development of an adjacent fruiting position. Dates were recorded for each leaf unroll, square seen, white bloom, and for square or boll abscission on observation plants. The mainstem node position of each branch and nodal position of each fruit were also recorded.

Early season square shedding was higher in 1976 than 1977 at both the first and second positions on a sympodium.

Although a late season decrease in the number of sympodia which developed two fruiting positions was observed both years, the decrease was much greater in 1977. The rapid decrease in 1977 represents earlier cut-out that year probably due to an earlier and heavier boll set. A heavy boll load creates a large demand for plant nutrients which may result in accumulation of carbohydrates at the expense of new growth.

Square shedding was lower and boll retention was higher at the first compared to the second position on a fruiting branch. First position fruit are closer to the mainstem and to the mainstem leaf subtending the fruiting branch and, therefore, in a more competitive position than fruit located at the second position. First position fruit are also at maximum sink strength when second position fruit are most susceptible to shed.

Percent boll shedding at the second position increased as the first position fruit was maintained longer. The second position set the highest percentage of bolls when the first position shed as a square. The fate of the second position appeared to have little effect upon boll retention at the first position.

Square period (days to white bloom) decreased at both positions during both seasons. The reason for this decrease is not clear, but may be related to increasing daily mean temperature or improving position of the squares on the plant in relation to light and temperature during the season. Shedding at the first position had no effect on the square period of the second position on that sympodium.

The competition between adjacent fruiting positions for plant nutrients was apparent in boll weights and fiber qualities. Second position bolls produced more seed cotton and tended to produce higher quality fiber when the first position shed than when it matured.

However, the seed cotton weight increases at the second position were not equivalent to that lost by abscission at the first position. Apparently only a portion of the carbohydrates made available by abscission at the first position were partitioned to the adjacent second position fruit. Further research is needed to determine how the plant responds to the freed assimilates and the extent genetic and environmental differences effect that response.

APPENDIX A

EFFECTS OF SHEDDING ON FRUITING POSITIONS

Table A-1. Relationship between shedding at the first position on a sympodium and the fate of the second position on the same sympodium for cotton grown in 1976. Values represent shedding percentages (square shed (SS), boll shed (SB), and boll retention (B)) of the first position based upon the fate of the second position (SS, SB, B). Values are from sympodia grouped into four mainstem node segments.

Condition		Percent First Position Shed						
		Mainstem Nodes 11-15				Mainstem Nodes 16-20		
		SS	SB	B		SS	SB	B
Fate of Second Position	SS	48	14	37	SS	24	25	51
	SB	30	16	54	SB	13	21	65
	B	39	18	53	B	28	23	49
		Mainstem Nodes 21-25				Mainstem Nodes 11-25		
		SS	SB	B		SS	SB	B
Fate of Second Position	SS	21	36	43	SS	34	23	23
	SB	12	29	59	SB	18	22	60
	B	22	35	42	B	31	24	45

Table A-2. Relationship between shedding at the first position on a sympodium and fate of the second position on the same sympodium for cotton grown in 1977. Values represent shedding percentages (square shed (SS), boll shed (SB), boll retention (B)) of the first position based upon the fate of the second position (SS, SB, B). Values are from sympodia grouped into four mainstem node segments.

Condition		Percent First Position Shed						
		Mainstem Nodes 11-15				Mainstem Nodes 16-20		
		SS	SB	B		SS	SB	B
Fate of Second Position	SS	19	22	59	SS	12	50	38
	SB	9	13	77	SB	7	29	64
	B	21	23	55	B	16	38	46
		Mainstem Nodes 21-25				Mainstem Nodes 11-25		
		SS	SB	B		SS	SB	B
Fate of Second Position	SS	32	50	18	SS	20	43	37
	SB	14	48	38	SB	9	23	68
	B	16	48	14	B	20	28	52

Table A-3. Effect of shed at the first position of a sympodium on the square period (days) of the second position from sympodia grouped into four mainstem node segments for cotton grown in 1976 and 1977. SS shed as a square, SB shed as a boll, B boll matured.*

	Mainstem Nodes											
	11-15			16-20			21-25			11-25		
	Fate of First Position											
	SS	SB	B	SS	SB	B	SS	SB	B	SS	SB	B
1976	20.1a	18.6b	19.6a	17.2	17.0	17.1	17.3	17.5	17.5	18.6a	17.6c	18.0b
1977	18.1	18.2	18.1	17.9	17.9	17.9	17.7	17.7	17.1	18.0	18.0	18.0

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[*] Means followed by the same letter within a mainstem node group do not differ by the Duncan-Multiple Range Test at the 0.05 level.

Table A-4. Effect of shedding at the first position on a sympodium on the second position seed/boll, percent lint, and fiber length, strength, and fineness for cotton during 1977.*

Sympodial Position	Seed/boll	% Lint	Length	Strength	Fineness
First	25.3	38.4	1.11	3.16	5.23
Second w/first position shed	25.4	37.9	1.11	3.15	4.98
Second w/first position present	24.2	37.5	1.11	3.11	4.74

*No significant differences were found using the Duncan-Multiple Range Test at the 0.05 level.

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