CAUSES OF SQUARE AND BOLL SHEDDING

Gene Guinn, Plant Physiologist (retired)
USDA, ARS, Western Cotton Research Lab
Phoenix, AZ

Abstract

Abscission or shedding occurs when the hydrolytic enzymes cellulase and pectinase weaken cell walls and middle lamellae of cells in the abscission zone at the base of the pedicel. Any condition that increases shedding must increase the activity of these enzymes. Hormones affect the synthesis of cellulase and pectinase in the abscission zone. IAA inhibits their synthesis whereas ethylene stimulates the synthesis of these hydrolytic enzymes. Ethylene also slows movement of IAA and causes its destruction by oxidative decarboxylation. ABA may also increase cellulase and pectinase activity by stimulating ethylene production (and possibly by a more direct effect).

Any condition that decreases the available supply of photosynthate increases square and boll shedding. These conditions can include dim light (due to cloudy weather and/or excessive leaf area), water deficit, high temperatures (day and/or night), deficiencies of inorganic nutrients required for photosynthesis or translocation of photosynthate from leaves to bolls, a heavy boll load, leaf-feeding insects, and diseases that cause injury to, or abscission of, leaves. Some evidence indicates that these conditions increase ethylene production and decrease IAA content of fruiting forms.

Other conditions that cause shedding include failure of pollination (e.g., due to excessively high temperatures or rain in the open flower), a deficiency of Zn that is required for the synthesis of IAA, and insects that feed and/or oviposit directly in squares and bolls.

Probability of shedding changes with age of the square or boll, with boll load during the season, and with position on the fruiting branch. Large squares are resistant to shedding, apparently because of very high concentrations of IAA. Young bolls (and probably young squares) are much more likely to shed because they contain much less IAA and readily produce large amounts of ethylene. Shedding decreases with boll age starting about a week after anthesis, presumably because of increasing amounts of IAA, a decrease in ability to produce ethylene, and increasing thickness of cell walls of cells in the abscission zone. Bolls rarely shed 3 weeks or more after anthesis even when damaged by bollworms.

Square and boll shedding increase with increasing boll load. But, shedding then decreases as older bolls mature and the "active boll load" decreases. Squares and bolls are most likely to be retained at the first node of fruiting branches.

The nutritional and hormonal theories are not mutually exclusive or contradictory. Environmental conditions affect hormonal balance which, in turn, regulates activity of the hydrolytic enzymes in the abscission zone that cause shedding.

Introduction

This subject was reviewed earlier in a USDA technical bulletin (Guinn, 1982b) and a book chapter (Guinn, 1986), but some additional information has been obtained since that time.

Yield can be affected by retention of squares and bolls. Early workers tended to ascribe shedding to one or a few factors. For example, Lloyd (1920) attributed variation in shedding of squares and bolls to variations in moisture supply. While moisture supply can certainly affect fruit retention, not all shedding can be attributed to drought.

Mason (1922) recognized the importance of photosynthesis. He noted that dark, rainy weather increased shedding, and leaf removal caused almost complete shedding of young bolls. According to Eaton (1955), this work marked the beginning of the nutritional theory of boll shedding which stated that "the cotton plant retains only as many bolls as it can supply with carbohydrates, nitrogen, or other nutrients." (Although sugars are commonly thought of as the form of organic nutrients supplied to bolls, amino acids and fatty acids are also important, especially for seed growth. Regardless of whether amino acids and fatty acids are translocated from leaves to bolls or are synthesized in bolls, the fixed carbon must come from photosynthesis.) Eaton and Rigler (1945) and Eaton and Ergle (1953, 1954) subsequently obtained results that could not always be explained by the nutritional theory. They suggested that "boll shedding is controlled by the balance between auxin produced in the leaves and an anti-auxin or inhibitory material from developing bolls." Much subsequent research concentrated on hormonal effects.

Research by Addicott and Carns and their co-workers led to the discovery of abscisic acid (ABA) (Carns et al., 1960; Liu and Carns, 1961; Addicott et al., 1964; Ohkuma et al., 1963, 1965). ABA appeared to have most of the anti-auxin properties postulated by Eaton and Ergle. It was found in bolls and counteracted the growth-promoting effects of auxin (Carns et al., 1960).

Hall and his students at Texas A & M concentrated on ethylene as a regulator of leaf and fruit abscission. Lipe and Morgan (1972, 1972) obtained convincing evidence that ethylene is a potent regulator of boll abscission.

Do the results with hormones indicate that the nutritional theory of boll shedding is invalid? Not at all. Results of several experiments indicate that increasing photosynthesis increases boll retention and yield (Guinn et al., 1976; Mauney et al., 1978; Faver and Gerik, 1996) My work indicated that hormonal balance is affected by environment and boll load, and also changes with age of squares and bolls. Therefore, the nutritional and hormonal theories of boll shedding are not contradictory or mutually exclusive; they just represent different parts of the overall control system.

In this presentation I will discuss enzymes and hormones involved in the abscission process; effects of light intensity, moisture supply, temperature, inorganic nutrients, insects, and diseases; changes in probability of shedding during the season; changes with age of individual fruiting forms; and effects of position on the fruiting branch.

Enzymes and Hormones

When a square or boll sheds, separation occurs at the base of the pedicel in an area of specialized cells called the abscission zone. Abscission is an active process that requires living tissue and active enzymes. Two hydrolytic enzymes, pectinase and cellulase, weaken the middle lamellae and cell walls, respectively, of cells in the abscission zone. Any condition that causes abscission (shedding) must affect the synthesis of one or both of these enzymes and their secretion through the plasma membrane. Two, or possibly three, hormones appear to have a direct effect on pectinase and cellulase.

It has been known for many years that auxin (indole-3-acetic acid, IAA) usually inhibits abscission if the concentration is higher in the distal than in the proximal (basal) side of the abscission zone. IAA prevents an increase in the specific cellulase that causes abscission (Abeles, 1969; Ratner et al., 1969; Lewis and Varner, 1970). Factors that slow movement of IAA to the abscission zone tend to promote abscission (Morgan and Durham, 1972).

Conversely, ethylene is a potent abscission-promoting hormone. It stimulates the synthesis of pectinase and cellulase in the abscission zone (Horton and Osborne, 1967; Abeles, 1968, 1969; Ratner et al., 1969; Abeles et al., 1971; Reid et al., 1971; Riov, 1974), apparently by promoting the synthesis of specific mRNAs (Tucker et al., 1988, 1991). Ethylene also destroys IAA (by oxidative decarboxylation) and slows its rate of movement to the abscission zone (Morgan et al., 1968; Beyer and Morgan, 1969, 1970, 1971).

ABA can also promote abscission, but its effect may be indirect because ABA can stimulate ethylene production (Craker and Abeles, 1969; Abeles et al., 1971; Jackson and Osborne, 1972; Sagee et al., 1980). ABA stimulated abscission of citrus leaves only when ethylene synthesis was not blocked with an inhibitor (Sagee et al., 1980). Some evidence, however, indicates that ABA may have direct effects that are not dependent upon increased ethylene production (Craker and Abeles, 1969; Cooper and Horanic, 1973).

Other hormones, such as cytokinins and gibberellins, may also affect abscission, but their effects appear to be less direct. Cytokinins delay or prevent senescence and promote the ability of an organ to compete for metabolites (Letham, 1967). Mosjidis et al. (1993) reported that application of a cytokinin to soybean pods increased metabolic activity, stimulated pod and ovule growth, and increased pod set. However, Varma (1976) reported that cytokinin treatments promoted boll abscission except when applied directly to the abscission zone. Osborne and Moss (1963) obtained similar results with bean explants and suggested that mobilization of nutrients away from the abscission zone would cause senescence there and promote abscission.

Results have also been variable with gibberellins. When Walhood (1957) applied GA directly to cotton fruits the treated fruits did not abscise, but untreated fruits on the same plant abscised at greater rates than those on control plants. When Johnson and Addicott (1967) applied GA to all fruits on the same plant there was no increase in retention. Cognee (1975) reported that gibberellin content remained low in bolls destined to abscise but increased in retained bolls. Application of GA to explants generally increases abscission (Carns et al., 1961; Morgan and Durham, 1975), possibly because of enhancement of ethylene action (Morgan and Durham, 1975). Experimental results and analyses of gibberellin content may be complicated by the fact that there are many gibberellins.

Although ABA, cytokinins, and gibberellins may indirectly affect abscission, IAA and ethylene appear to be the hormones that are most consistently and directly involved in controlling abscission. Additional research is needed on possible changes in cytokinins (and possibly gibberellins) during the season as boll load increases and root growth decreases (Crowther, 1934; Eaton and Joham, 1944) because roots are generally recognized as a major site of cytokinin synthesis.

Environmental Factors

Many environmental factors can increase square and boll shedding, apparently by affecting the hormonal balance which, in turn, regulates pectinase and cellulase activity in the abscission zone.

Irradiance
Several workers have shown that low light intensity increases square and boll shedding (Mason, 1922; Dunlap, 1945; Eaton and Rigler, 1945; Saad, 1951; Eaton and Ergle, 1953; Goodman, 1955; Sorour and Rassoul, 1974; Guinn,

1976a; Vaughan and Bate, 1977; Pettigrew, 1994; Crozat et al., 1997), presumably because it slows photosynthesis and decreases the supply of organic nutrients. Plants with the heaviest boll load are the most sensitive to dim light (Goodman, 1955), probably because of their heavy demand for photosynthates.

Cloudy weather is just one of the factors that can decrease light intensity. Conditions that increase leaf area index (LAI) can increase mutual shading and decrease light intensity in the canopy. For example, abundant moisture and nitrogen increase growth and leaf size (Boyer, 1976; Radin and Mauney, 1986). A high plant population further increases LAI and mutual shading. Eaton and Rigler (1945) noted that the combination of close spacing, fertile soils, and abundant moisture greatly decreased relative fruitfulness. Excesssively high plant populations can cause a high percentage of the plants to become barren (Peacock et al., 1971). Brown (1971) reported that buds, bolls, and total fruiting positions decreased as population increased with the effect being most pronounced in the bottom third of the plant canopy. Shedding increased with increasing plant population. Gerard and Reeves (1974, 1975) and Gerard et al., 1976a, b) reported that a combination of high plant population (320,000 plants/ ha), abundant soil moisture, excess N, and a sandy loam soil increased square shedding, increased vegetative growth, and caused a marked reduction in yield. I have seen similar conditions on fertile Delta soils in NE Arkansas where plants were over six feet tall but had few bolls. Plants in a nearby field at a much lower population were shorter and had a heavy boll load. Pettigrew (1994) not only determined the effects of shading, which decreased boll retention and yield, but also compared the effects of reflectors and opening the canopy to increase light intensity. Even with a low population of 65,000 plants/ha, opening the canopy increased boll retention and yield. Reflectors also increased number of bolls and yield, although not as much as did opening the canopy (because reflectors increased irradiance for only a relatively brief time).

Guinn (1985b) removed plants to increase light penetration at different stages of development. Thinning at three weeks after first flower caused an immediate increase in boll retention and a subsequent increase in flowering rate. Thinning at first square or at first flower also greatly increased flowering rate compared to the control. These results, and those of Kerby and Buxton (1978) and Heitholt (1995), indicate that crowding may decrease the production of fruiting sites and retention of squares. Heitholt (1995) compared flowering, boll retention, and yields of plants grown at populations that varied from 2 to 20 plants/square m. Increasing plant population did not decrease boll retention in his experiment but did decrease number of flowers per plant. Except for okra-leaf plants at 2 vs. 3 plants/square m, the number of flowers produced per square m of land was about the same for all plant populations, thus indicating that the number of flowers per plant decreased

with increasing plant population. In an earlier report, Heitholt (1984a) stated that yield decreased when LAI exceeded 5. Neither his data nor mine indicated relative effects on fruiting site production and square retention with increasing plant population, but both were probably affected. Crowded plants tend to have small fruiting branches, and some weak plants appear to have none.

Dim light would decrease photosynthesis and, thus, the supply of photosynthate. This deficiency of photosynthate is probably a major cause of reduced fruit retention under low-light conditions. However, sugar content does not always correlate with fruit shedding. Heitholt and Schmidt (1994) compared sugar contents of large squares, ovaries of flowers, and ovaries of young bolls with shedding rates of 9 genotypes at different positions on fruiting branches and found no significant correlations between sugar contents and shedding rates.

Guinn and Brummett (1987) thinned plants to increase light intensity (and thus photosynthesis) and removed all bolls to decrease the demand for photosynthate. Three-day old bolls were subsequently harvested and analyzed for ABA and IAA to see if hormonal changes might account for changes in boll retention. Thinning and defruiting increased boll weight and boll retention, decreased the ABA content of bolls, and increased the IAA content of abscission zones at all three harvest dates. Boll retention rate was negatively correlated with ABA content of bolls and positively correlated with IAA content of abscission zones. Ethylene was not measured in this experiment, but was measured in an earlier experiment in which plants were defruited and subjected to periods of dim light (Guinn, 1976a). Dim light increased, and defruiting decreased, ethylene production. Thus, dim light changed all three hormones (ABA, IAA, and ethylene) in ways that should decrease boll retention.

Water

Either too much or too little water can cause shedding. Rain can rupture pollen and increase shedding if it occurs in the morning before pollination occurs. The poorly pollinated flowers subsequently shed (Lloyd, 1920; King et al., 1956) because they contain few fertilized ovules which probably produce IAA, cytokinins, and gibberellins (Luckwill, 1954; Bhardwaj et al., 1975). Even without rain, cloudy weather can increase square and young boll shedding by decreasing photosynthesis. (See previous section on irradiance.)

Too much water can cause shedding because of inadequate aeration of roots, especially in heavy soils (Longenecker and Erie, 1968). Anaerobic soil conditions may increase ethylene production by increasing the production of 1-aminocyclopropane-1-carboxylic acid (ACC, an immediate precursor of ethylene) in roots. The production of ACC does not require oxygen, but its conversion to ethylene does. Therefore, when ACC that accumulates in oxygen-deprived roots moves to the tops (where there is plenty of oxygen) the ACC is then converted to ethylene and may increase

shedding (Bradford and Yang, 1980). The only time I have seen white blooms shed was shortly after a heavy irrigation during hot weather when the water stood for several hours.

There is some disagreement in the literature regarding the optimum moisture supply for cotton. A few reports give the impression that fruiting can be stimulated by a mild water deficit (Harris and Hawkins, 1942; Singh, 1975; Kittock, 1979). Two factors may be involved. High humidity and abundant soil moisture stimulate leaf growth and increase mutual shading which can decrease the production and retention of squares (see section on irradiance). However, this probably occurs only in crowded plants. Abundant soil moisture and N do not decrease flowering when the plant population is low. The other factor is plant bugs, which are favored by frequent irrigation and high plant populations (Leigh et al., 1974; Guinn and Mauney, 1984). These plant bugs preferentially feed on small squares and cause them to shed (Mauney and Henneberry, 1984; Flint et al., 1989; Stewart and Sterling, 1989), thereby causing a subsequent decrease in flowering rate.

Large squares do not shed readily due to water deficit early in the season and flowers seldom shed (Ewing, 1918; McNamara et al., 1940; Eaton and Ergle, 1953; Guinn and Mauney, 1984). Therefore, young plants continue to flower even when severely stressed. Because of smaller, and wilted, leaves it is easier to see the flowers. This may lead to the often erroneous assumption that water-deficit stress stimulates flowering. Guinn and Mauney (1984) delayed irrigation in one treatment from May 28 to July 8 and found that flowering continued unabated through July 3 even though midday leaf water potential had declined to near -3.0 MPa. Flowering rate then started to decline and continued declining after irrigation on July 8 and 15. This could be misinterpreted as indicating that irrigation inhibited flowering. Flowering rate increased rapidly after July 29 (three weeks after irrigation). The decline in flowering after irrigation occurred because small squares had aborted during severe stress. When stress was relieved, pinhead squares were then retained but did not appear as flowers until three weeks later. Drought also causes severe young boll shedding (Ewing, 1918; Lloyd, 1920; Guinn and Mauney, 1984). Therefore, despite continued flowering during stress, a severe water deficit in the early flowering stage is doubly harmful; it causes an immediate loss of many young bolls and then decreases flowering later because of loss of small squares. Stockton et al. (1961), Bruce and Romkens (1965), and Lashin et al. (1970) reported increased flowering with increased irrigation. Stress typically does not develop rapidly before the pinhead square stage because the plants are still small and have a relatively low transpiration rate.

Water deficit decreases net photosynthesis in a number of ways, e.g., by decreasing leaf growth and area (Boyer, 1973; Marani and Levi, 1973), by causing stomatal closure (Jordan et al., 1975; Boyer, 1976; Cutler and Rains,

Ackerson et al., 1977; McMichael and Hesketh, 1977), by decreasing the synthesis and activity of photosynthetic enzymes (Jones, 1973), by decreasing photophosphorylation (Boyer, 1973) and Hill reaction activity (Fry, 1970), by increasing photorespiration (Lawlor and Fock, 1975; Lawlor, 1976), and by increasing leaf senescence and abscission (McMichael et al, 1973).

A decrease in net photosynthesis may cause a deficiency of assimilate that can affect hormonal status, as noted above. In addition, water deficit may directly affect hormonal balance in squares and bolls. It is well known that drought increases the ABA content of leaves. Water deficit also increased the ABA content of squares and flowers (Guinn et al, 1990) and bolls (Guinn, 1982a; Guinn and Brummett, 1987), increased IAA oxidase activity (Darbyshire, 1971), appeared to decrease the IAA content of boll abscission zones (Guinn and Brummett, 1987), and increased ethylene production in young bolls (Guinn, 1976b). To what extent these hormonal changes were caused directly by water deficit versus a decrease in photosynthesis is not readily apparent except that Guinn (1976b) found marked increases in ethylene production in isolated bolls that were desiccated over silica gel compared to those kept in moist containers. Conversely, Morgan et al. (1990) reported that water-deficit stress did not promote ethylene synthesis of intact plants or their attached bolls. Possible reasons for the different results are not readily apparent, but their results weaken the hypothesis that water deficit increases shedding by increasing ethylene production.

Whatever the mechanism(s), water deficit is a potent and common cause of shedding.

Temperature

Cotton is more heat tolerant than many C3 plants. However, excessively high temperatures increase square and boll shedding and decrease yield (Dunlap, 1945; Powell, 1969; Bhatt et al., 1972; Fisher, 1973; Guinn, 1974a; Kuehl et al., 1976; Bhatt and Nathan, 1977; Brown et al., 1995; Zeiher et al., 1995). High temperature can decrease the supply of photosynthate by increasing the rates of photorespiration (Laing et al., 1974; Ku and Edwards, 1977; Krieg, 1986) and dark respiration (Guinn, 1974a), and thereby cause a nutritional stress. A nutritional stress increased ethylene evolution by young bolls (Guinn, 1976a). High temperature may induce callose formation in phloem and thereby decrease translocation of organic nutrients (McNairn, 1972). High temperature can also prevent the production of viable pollen (Meyer, 1969; Powell, 1969; Fisher, 1975) and thereby cause young boll abortion.

About the only practical way of lowering temperature is by irrigating (if possible) to maintain transpiration and, thus, evaporative cooling.

Low temperatures slow development but do not cause shedding.

Inorganic Nutrients

Effects of inorganic nutrients on abscission and relative fruitfulness were reviewed earlier (Addicott and Lyon, 1973; Guinn, 1982b; Joham, 1986) and will only be summarized here.

A deficiency of inorganic nutrients may increase shedding by decreasing photosynthesis, by decreasing translocation of photosynthate, or by directly affecting the synthesis of hormones. In many cases, the roles of nutrients are so extensive that a deficiency may decrease growth and the production of fruiting sites without a measurable decrease in retention of the few fruiting forms produced.

Nitrogen, P, K, Mg, S, Fe and Zn are required for photosynthesis and other essential metabolic processes. However, deficiencies may limit growth and the production of fruiting sites so much that measurable increases in shedding of squares and bolls are not evident (Wadleigh, 1944). Effects of nutrients on leaf area and mutual shading can confound results. For example, N is required for photosynthesis (Nevins and Loomis, 1970) and is a component of IAA and cytokinins. Therefore, a N deficiency can increase abscission (Addicott and Lynch, 1955; Addicott and Lyon, 1973) and decrease growth and yield. However, adequate to excess N, especially in combination with abundant moisture and close spacing, can increase shedding and decrease yields because of decreased light intensity in the canopy (Gerard and Reeves, 1975; Gerard et al., 1976a,b). (See previous section on irradiance.) A lower plant population, to allow better light penetration, is the obvious answer to problems caused by excessively high LAI.

Ca, K, and B are required for the transport of assimilates from leaves to fruiting forms (Eaton, 1955; Joham, 1986). Joham (1957) reported that a severe Ca deficiency caused complete failure of cotton plants to set bolls. B is also required for healthy phloem and the transport of sugars. Several workers reported that B deficiency increases shedding of squares and bolls (Eaton, 1932; Page and Bergeaux, 1961; Lancaster et al., 1962; Hinkle and Brown, 1968). A mild B deficiency may not slow vegetative growth but may, instead, produce a rank growth in which few bolls are set (Hinkle and Brown, 1968). Eaton (1932) found that cotton had a higher B requirement than any of 59 other plants tested. However, modern cultivars may not require as much B as older cultivars. Heitholt (1994b) found no effect of soil or foliar applications of B on number of flowers, boll retention, and yield of five modern genotypes.

A Zn deficiency results in smaller leaves (Hewitt, 1963) and also limits photosynthesis per unit of leaf area (Ohki, 1976). In addition, Zn deficiency may increase shedding because Zn is required for IAA synthesis (Skoog, 1940; Tsui, 1948).

Insects

Insects may increase square and boll shedding by direct damage to the fruiting form or by decreasing photosynthate by feeding on leaves. Detection and identification of insect damage to small squares may require microscopic examination (Mauney and Henneberry, 1979, 1984). This lack of obvious visible symptoms may have been a major reason for earlier disagreement about causes of loss of small squares.

Thrips, *Frankliniella* spp., can introduce bacteria that cause soft rot in small squares and cause them to shed (Mauney et al., 1980; Flint et al., 1989). Several plant bugs such as lygus bugs *(Lygus hesperus* Knight), tarnished plant bugs *(Lygus lineolaris* [Palisot and Beauvois]), and the cotton fleahopper *(Pseudatomoscelis seriatus* [Reuter]) can also cause small squares to shed (Mauney and Henneberry, 1979, 1984; Flint et al., 1989; Stewart and Sterling, 1989).

Boll weevils, *Anthonomus grandis* Boheman, feed upon and deposit their eggs in large squares (and young bolls when squares are scarce). Oviposition causes the bracts to flare and the squares and young bolls to turn yellow and abscise (Coakley et al. 1969).

The cotton bollworm, *Heliothis zea* (Boddie), and the tobacco budworm, *H. virescens* (Fabricius), deposit their eggs on young leaves and growing points. After hatching, the worms progress from squares to young bolls to older bolls as they grow and move down the plant. Older bolls may not shed (Stewart and Sterling, 1989) even though heavily damaged. (See later section on square and boll age.)

The pink bollworm adult, *Pectinophora gossypiella* (Saunders), may oviposit on leaves, squares, or young bolls, but prefers older bolls. Larval feeding in older bolls rarely causes them to abscise unless there are several larvae in each boll (Fry et al., 1978).

Ethylene is probably a cause of increased shedding when insects feed on or oviposit in squares and bolls. Physical injury increases ethylene production; I have never seen a young boll with evidence of insect feeding that did not produce abnormally large amounts of ethylene (Guinn, unpublished).

Leaf feeding insects such as the cotton leafperforator, *Bucculatrix thurberiella* Busck, the cotton leafworm, *Alabama argillacea* (Hubner), the cabbage looper, *Trichoplusia ni* (Hubner), the salt-marsh caterpillar, *Estigmene acrea* (Drury), the beet armyworm, *Spodoptera exigua* (Hubner), and the yellow-striped armyworm, *Spodoptera ornithogalli* (Guenee), can increase shedding by destroying photosynthetic tissue and decreasing available photosynthate. Spider mites, *Tetranchyus* spp., cause leaf abscission and decrease photosynthesis.

Diseases

Diseases may cause infection and rotting of bolls, moisture deficit (due to xylem blockage), or leaf damage and defoliation.

Bacterial blight, *Xanthomonas malvacearum* (E. F. Sm.) Dows., and anthracnose boll rot, *Glomerella gossypii* (South.) cause direct damage to, and shedding of, young bolls. Close spacing and humid conditions increase the severity of boll rots. Fortunately, cultivars have been developed that are resistant or immune to bacterial blight (Brinkerhoff, 1970).

Verticillium wilt, *Verticillium albo-atrum* (Reinke and Berth.), is a disease in which the fungus grows in and partially obstructs the xylem, thereby causing the plants to wilt. The leaves also develop chlorotic areas and may abscise. Severely affected plants shed all of their leaves and most of their bolls (Presley, 1953), probably because of a doubling of the ABA content of leaves and a fivefold increase in their ethylene evolution (Wiese and DeVay, 1970). Fusarium wilt, *Fusarium oxysporum* Schlect. *F. vasinfectum* (Atk.) Snyd. and Hans., causes symptoms similar to those caused by verticillium wilt. Bolls that do not shed are small and contain poor quality lint (Smith, 1953).

The leaf spots caused by *Alternaria tenuis* Nees and *Ascochyta gossypii* Woron. can cause leaf abscission and resulting starvation of squares and young bolls. A plant infected with *A. gossypii* may lose most of its leaves and fruiting forms, and may even die (Blank, 1953).

Square and Boll Age

Unless damaged by insects, large squares seldom shed and open flowers almost never shed (Ewing, 1918; McNamara et al., 1940; Eaton and Ergle, 1953; Guinn and Mauney, 1984). Conversely, young bolls are likely to shed; the most susceptible stage is during the week following anthesis. Shedding percentage then decreases with boll age until bolls are almost immune to shedding by 3 weeks after anthesis (Guinn, 1982c, 1986).

A low rate of shedding of large squares may be due to their high IAA content. Total IAA content reached a maximum approximately 6 days before anthesis and then decreased rapidly to a minimum at 2 days after anthesis (Guinn and Brummett, 1989a). The reason for this rapid and marked decrease in IAA is not known. (Perhaps IAA is used in the rapid growth of the corolla.) Shedding of young bolls started 2 days after anthesis, reached a maximum at 5 to 6 days after anthesis and then declined rapidly as the IAA content of bolls increased. Decreases and increases in IAA slightly preceded increases and decreases in shedding rate. This slight delay in response is to be expected because some time is required for IAA to affect the synthesis of cellulase and pectinase, for these hydrolytic enzymes to be synthesized and secreted through the plasma membrane, and for them to partially hydrolyze and weaken the cell wall and middle lamella of cells in the abscission zone.

Changes in rate of ethylene production also appear to be involved in changes in shedding rate. Lipe and Morgan (1972, 1973) found maximum rates of ethylene evolution at anthesis (just before the rapid increase in rate of boll shedding). I measured changes in ability to produce ethylene by wounding bolls that were from 4 to 14 days old (Guinn, 1982c). Ability to produce ethylene declined steadily with age to about 1/10 the rate measured at 4 days after anthesis. The combination of increasing IAA and decreasing ethylene, with boll age, should decrease shedding rate as bolls grow (because IAA inhibits and ethylene promotes abscission).

Davis and Addicott (1972) measured ABA and suggested that changes in ABA might be responsible for changes in rate of boll shedding. However, they found maximum concentrations of ABA at 10 days post anthesis, well after the maximum rate of boll shedding we found (Guinn and Brummett, 1988). Davis and Addicott (1972) reported cumulative rather than daily rates of boll shedding. Therefore, boll age for maximum shedding is not readily apparent in their data.

Structural changes may also be involved in the decreasing susceptibility of bolls to shed with increasing age. Cell walls thicken and become more resistant to hydrolytic breakdown. Treatment with Ethrel ([2-chloroethyl] phosphonic acid) caused the formation of an open abscission layer around the pedicel of mature bolls, but the pedicel did not break, apparently because the woody xylem cells were not dissolved (P. W. Morgan, pers. communication). It is fortunate that mature bolls do not shed (e.g., like ripe apples). Separation does occur, however, between locules as dehiscence and boll opening occur.

Changes During the Season

Rates of square and boll shedding increase during the season (Lloyd, 1920; McNamara et al., 1940; Davis and Addicott, 1972; Ehlig and LeMert, 1973; Verhalen et al., 1975; Patterson et al., 1978; Guinn and Mauney, 1984; Guinn, 1985b). Lloyd (1920) and McNamara et al. (1940) suggested that depletion of soil moisture was responsible for the seasonal decline in boll retention. Others have suggested that high temperatures were responsible for increased shedding during the season (Zeiher, et al., 1995). However, Ehlig and LeMert (1973), Patterson et al. (1978), and Guinn (1985b) showed that partial defruiting delayed the normal increases in boll shedding. Guinn and Mauney (1984) and Guinn (1985b) found that rate of boll retention started decreasing shortly after the start of flowering. Retention rate continued to decline with increasing boll load. However, boll retention rate started increasing as

soon as older bolls started maturing more rapidly than new bolls were being added. (We referred to this as a decrease in active boll load, i.e., the number of immature bolls per plant).

Changes in hormonal balance could be responsible for increased shedding with increasing boll load. Decreases in growth and flowering accompany decreases in boll retention as boll load increases. According to Ewing (1918), W. L. Balls ascribed the cessation of growth and flowering to senescence caused by "self-poisoning." Davis and Addicott (1972) found much higher concentrations of ABA in abscised than in retained bolls late in the season when the shedding rate was high. In contrast, Guinn (1982a, 1985a) found a slight but not a consistent effect of boll load on the ABA content of bolls and no effect on the ABA contents of fruiting branches and mainstem apices (Guinn, 1985a). Likewise, Guinn and Brummett (1992) found almost no effect of defruiting on the ABA content of leaves. Thinning and defruiting did cause a slight decrease in the ABA content of 3-day-old bolls and a slight increase in the IAA content of their abscission zones (Guinn and Brummett, 1987). ABA content increased and IAA decreased from July 8 to July 15, possibly due to increasing water deficit during an irrigation cycle. Limited data obtained with field-grown plants indicated that ethylene evolution from 4-day-old bolls increased through August 6 and then declined as older bolls started to mature (Guinn, 1976a). These results, however, were confounded by changing moisture status during irrigation cycles and a hail storm on August 6. More research is needed to determine changes in the ABA and IAA contents of bolls and their abscission zones, and on ethylene evolution from bolls, during the season as boll load increases and boll retention decreases.

Competition for organic and inorganic nutrients is almost certainly an important factor in causing increased shedding as boll load increases. Older bolls appear to be stronger sinks (are more competitive) than young bolls (Peoples and Matthews, 1981). Shedding of young bolls increased when demand for carbohydrates exceeded the supply (Hearn, 1972). Effects of dim light on boll shedding increased as boll load increased (Goodman, 1955), probably because the supply of photosynthates was already depleted by the heavy demand of the boll load.

Depletion of N may be another factor in decreasing growth, flowering, and boll retention as boll load increases. Bolls require N for growth of seeds. However, N uptake is decreased because root growth decreases with increasing boll load (Eaton, 1931; Crowther, 1934; Eaton and Joham, 1944). Crowther (1934) reported that N uptake essentially ceased when the plants set a heavy boll load even though the soil still contained N. It is well known that petiole nitrate content decreases greatly during the season. G. C. Bate and coworkers (pers. communication) believe that N availability is a major factor in regulating boll shedding. Jones et al. (1974) developed a computer simulation model

in which N supply is a major factor in regulating growth and the shedding of squares and bolls. An adequate supply of N delays the decreases in growth, flowering, and fruit retention that lead to cutout (Tucker and Tucker, 1968; Hearn, 1975).

Position on the Fruiting Branch

Most of the retained bolls are borne on the first node (Mauney, 1979; Kerby and Buxton, 1981; Peoples and Matthews, 1981). Mauney (1979) reported that 73% of matured bolls were borne on the first nodes, 24% on the second, and only 2% on the third. Relative retention rates vary with spacing, cultivar, and environment.

Several possible reasons for the marked difference in retention at different nodes can be suggested:

1. Young bolls obtain most of their photosynthate from subtending leaves and lesser amounts from leaves at adjacent nodes (Ashley, 1972). Bolls at adjacent nodes compete with each other (Kerby and Buxton, 1981; Peoples and Matthews, 1981). Because boll age varies about 7 days between fruiting-branch nodes (Kerby and Buxton, 1978) and competitive ability increases with boll age (Peoples and Matthews, 1981), the older bolls nearer the main stem have a competitive advantage.

2. Bolls at the first node can obtain some of their photosynthate from mainstem leaves. However, younger bolls at nodes 2 and 3 have less access to that source (Ashley, 1972; Peoples and Matthews, 1981).

3. Leaf size, and thus photosynthetic area, tends to decrease at progressive nodes out the fruiting branch.

4. Mutual shading increases with time at a given fruiting branch. Therefore, bolls that develop at nodes 2 and 3 do so in less favorable light conditions (see section on irradiance). Because of this effect, very high plant populations may greatly reduce boll setting beyond the first node of fruiting branches (Kerby and Buxton, 1981).

5. Nitrogen and other inorganic nutrients may be delivered in smaller amounts to more distant nodes.

Summary and Conclusions

Many environmental factors affect square and boll shedding. Most of them have one thing in common; they cause a stress, either nutritional or physical. Those that cause a nutritional stress can affect the supply of organic nutrients by affecting photosynthesis, photorespiration, dark respiration, or transport of assimilates from leaves to

fruiting sites. A deficiency of assimilates alters hormonal balance in squares and young bolls in ways that then increase activity of cellulase and pectinase in their abscission zones. These hydrolytic enzymes digest the cell walls and middle lamellae of cells in the abscission zone, resulting in separation. Hormonal balance can also be affected and shedding increased by the stress of physical injury (e.g., caused by insects, diseases, pollen rupture due to rain in open flowers, or by hail).

Ethylene is probably the most potent hormone that causes abscission. It is a "stress" hormone. Almost any kind of stress, whether nutritional or physical, increases its production and, thus, increases shedding. ABA is another stress hormone (responds strongly to water deficit), but apparently affects shedding mainly by stimulating ethylene production. IAA, on the other hand, tends to decrease or prevent the synthesis of cellulase and pectinase and, thus, decrease shedding.

Young squares and young bolls are more likely to shed than older squares and bolls, apparently because of changes in hormonal balance and increases in cell wall thickness with age of fruiting forms.

Shedding rate increases during the season, mainly due to increasing demand for photosynthates and N by the developing boll load (although depletion of soil moisture and N, high temperatures, and insect buildups can also play roles). This deprives the less competitive young squares, young bolls, growing points, and roots of needed nutrients.

Retention rate is greater at the first node of fruiting branches than at second or third nodes because of a competitive advantage and higher irradiance during the most vulnerable stage of growth.

In addition to controlling insects and diseases, genetic improvement and cultural practices to increase photosynthesis are probably the best ways to set more bolls and increase yields. Particular attention should be paid to the interactions of soil fertility, N, moisture supply, and plant population in affecting LAI and light intensity in the plant canopy. Despite their normally beneficial effects, adequate to excess N and soil moisture can decrease boll setting and yield when plant populations are too high for the conditions. Therefore, plant population should be limited so that spacing is adequate to prevent excessive mutual shading and low light intensity in the canopy.

References

Abeles, F. B. 1969. Abscission: role of cellulase. Plant Physiol. 44:447-452.

Abeles, F. B., G. R. Leather, L. E. Forrence, and L. E. Craker. 1971. Abscission: regulation of senescence, protein synthesis, and enzyme secretion by ethylene. Hortscience 6: 371-376.

Addicott, F. T., H. R. Carns, J. L. Lyon, O. E. Smith, and J. L. McMeans. 1964. On the physiology of abscisins. In *Regulateurs Naturels de la Croissance Vegetale,* J. P. Nitsch, ed., 687-703. Centre National de la Recherche Scientifique, Paris.

Addicott, F. T. and R. S. Lynch. 1955. Physiology of Abscission. Annu. Rev. Plant Physiol. 6:211-238.

Addicott, F. T. and J. L. Lyon.1973. Physiological ecology of abscission. In *Shedding of Plant Parts*, T. T. Kozlowski, ed., 85-124. Academic Press, New York and London.

Ackerson, R. C., D. R. Krieg, C. L. Harding, and N. Chang, 1977. Effects of plant water status on stomatal activity, photosynthesis, and nitrate reductase activity of field grown cotton. Crop Sci. 17:81-84.

Ashley, D. A. 1972. 14C-labelled photosynthate translocation and utilization in cotton plants. Crop Sci. 12:69-74.

Beyer, E. M., Jr. and P. W. Morgan. 1969. Ethylene modification of an auxin pulse in cotton stem sections. Plant Physiol. 44:1690-1694.

Beyer, E. M., Jr. and P. W. Morgan. 1970. Effect of ethylene on the uptake, distribution, and metabolism of indoleacetic acid-1-14C and -2-14C and naphthaleneacetic acid-1-14C. Plant Physiol. 46:157-162.

Beyer, E. M., Jr. and P. W. Morgan. 1971. Abscission: the role of ethylene modification of auxin transport. Plant Physiol. 48:208-212.

Bhardwaj S. N., I. S. Dua, and V. Nath. 1975. Boll shedding in cotton. VII. Role of growth regulating substances. Indian J. Plant Physiol. 18:127-130.
Bhatt, J. G. and A. R. S. Nathan. 1977. Studies on the growth of *G. barbadense* cottons in India. II. Responses to environmental stresses. Turrialba 27:83-92.

Bhatt, J. G., T. Ramanujam, and A. R. Seshadrinathan. 1972. Estimate of loss of the floral forms in cotton. Indian J. Agric. Sci. 42:210-214.

Blank, L. M. 1953. The leaf spots of cotton. In *Plant Diseases. The Yearbook of Agriculture*, A. Stefferud, ed., 315-317. U. S. Dept. Agric., Washington, D. C.

Boyer, J. S. 1973. Response of metabolism to low water potentials in plants. Phytopathology 63:466-472.

Boyer, J. S. 1976. Photosynthesis at low water potentials. Philosophical Transactions of the Royal Society of London. B. Biol. Sciences 273:501-512.

Bradford, K. J. and S. F. Yang. 1980. Xylem transport of 1-aminocyclopropane-1-carboxylic acid, an ethylene precursor, in waterlogged tomato plants. Plant Physiol. 65:322-326.

Brinkerhoff, L. A. 1970. Variation in *Xanthomonas malvacearum* and its relation to control. Annu. Rev. Phytopath. 8:85-110.

Brown, K. J. 1971. Plant density and yield of cotton in northern Nigeria. Cotton Gro. Rev. 48:255-266.

Brown, P. W, C. A. Zeiher, and J. C. Silvertooth. 1995. Response of upland cotton to elevated night temperatures: I. Results of field studies. Proceedings Beltwide Cotton Conferences. 1129.

Bruce, R. R. and M. J. M. Romkens. 1965. Fruiting and growth characteristics of cotton in relation to soil moisture tension. Agron. J. 57:135-140.

Carns, H. R., J. L. Lyon, and B. J. Counts. 1960. Fruit abscission induced by application of an abscission accelerating hormone to cotton. Proceedings 14th Cotton Defoliation-Physiology Conference. 8-10.

Carns, H. R., F. T. Addicott, K. C. Baker, and R. K. Wilson. 1961. Acceleration and retardation of abscission by gibberellic acid. 4th Internat'l. Conf. Plant Growth Regulation. 559-566. Iowa State Univ. Press, Ames, Iowa.

Coakley, J. M., F. G. Maxwell, and J. N. Jenkins. 1969. Influence of feeding, oviposition, and egg and larval development of boll weevil on abscission of cotton squares. J. Econ. Ent. 62:244-245.

Cognee, M. 1976. Variations in the physiological and hormonal states of cotton fruit and their relationship with the initiation of abscission. Ph.D. thesis. Univ. of Paris. 245 pp. (Translated from French by E. E. King)

Cooper, W. C. and G. Horanic. 1973. Induction of abscission at hypobaric pressures. Plant Physiol. 51:1002-1004.

Craker, L. E. and F. B. Abeles. 1969. Abscission: role of abscisic acid. Plant Physiol. 44:1144-1149.

Crozat, Y., V. Judais, and P. Kasemsap. 1997. Survival of cotton fruiting forms after a temporary light reduction as affected by fruit age and plant structure. Proceedings Beltwide Cotton Conferences. 1432-1435.

Crowther, F. 1934. Studies in growth analysis of the cotton plant under irrigation in the Sudan. I. The effects of different combinations of nitrogen applications and water supply. Ann. Bot. 48:877-913.

Cutler, J. M. and D. W. Rains. 1977. Effects of irrigation history on responses of cotton to subsequent water stress. Crop Sci. 17:329-335.

Darbyshire, B. 1971. Changes in indoleacetic acid oxidase activity associated with plant water potential. Physiol. Plant. 25: 80-84.

Davis, L. A. and F. T. Addicott. 1972. Abscisic acid: correlations with abscission and with development in the cotton fruit. Plant Physiol. 49:644-648.

Dunlap, A. A. 1945. Fruiting and shedding of cotton in relation to light and other limiting factors. Texas Agricultural Experiment Station Bulletin No. 677.

Eaton, F. M. 1931. Root development as related to character of growth and fruitfulness of the cotton plant. J. Agric. Res. 43:875-883.

Eaton, F. M. 1932. Boron requirements of cotton. Soil Sci. 34:302-305.

Eaton, F. M. 1955. Physiology of the cotton plant. Annu. Rev. Plant Physiol. 6:299-328.

Eaton, F. M. and D. R. Ergle. 1953. Relationship of seasonal trends in carbohydrate and nitrogen levels and effects of girdling and spraying with sucrose and urea to the nutritional interpretation of boll shedding in cotton. Plant Physiol. 28:503-520.

Eaton, F. M. and D. R. Ergle. 1954. Effects of shade and partial defoliation on the growth, fruiting, and fiber properties of cotton plants. Plant Physiol. 29:39-49.

Eaton, F. M. and H. E. Joham. 1944. Sugar movement to roots, mineral uptake, and the growth cycle of the cotton plant. Plant Physiol. 19:507-518.

Eaton, F. M. and N. E. Rigler. 1945. Effects of light intensity, nitrogen supply, and fruiting on carbohydrate utilization by the cotton plant. Plant Physiol. 20:380-411.

Ehlig, C. F. and R. D. LeMert. 1973. Effects of fruit load, temperature, and relative humidity on boll retention of cotton. Crop Sci. 13:168-171.

Ewing, E. C. 1918. A study of certain environmental factors and varietal differences influencing the fruiting of cotton. Mississippi Agricultural Experiment Station Bulletin No. 8.

Faver, K. L. and T. J. Gerik. 1996. Can cotton yield be increased by improving photosynthetic capacity? Beltwide Cotton Conferences. 1189.

Fisher, W. D. 1973. Association of temperature and boll set. Proceedings 25th Cotton Improvement Conference. 72-73.

Fisher, W. D. 1975. Heat induced sterility in upland cotton. Proceedings 27th Cotton Improvement Conference. 85.

Flint, H. M., F. D. Wilson, and N. J. Parks. Causes of square shed in cotton in central Arizona. Southwestern Entomologist. 14:271-278.

Fry, K. E. 1970. Some factors affecting the Hill reaction activity in cotton chloroplasts. Plant Physiol. 45:465-469.

Fry, K. E., D. L. Kittock, and T. J. Henneberry. 1978. Effects of number of pink bollworm larvae per boll on yield and quality of Pima and Upland cotton. J. Econ. Ent. 71:499-502.

Gerard, C. J. and S. A. Reeves. 1974. Influence of climatic conditions, soils and management on performance of different cotton types. Proceedings 26th Cotton Improvement Conference. 77-78.

Gerard, C. J. and S. A. Reeves. 1975. Influences of N and plant population on earliness and yields of early maturing cotton cultivars grown on irrigated vertisols. Proceedings 27th Cotton Improvement Conference. 78-80.

Gerard, C. J., B. W. Hipp, and S. A. Reeves, Jr. 1976a. Influence of previous cropping and irrigation on fruiting, fruit shedding and yields of early and late maturing cottons grown under sub-tropical conditions. Proceedings 28th Cotton Improvement Conference. 93-95.

Gerard, C. J., B. W. Hipp, and S. A. Reeves, Jr. 1976b. Influence of stress on growth and fruiting of early and late maturing cottons grown under sub-tropical conditions. Proceedings 28th Cotton Improvement Conference. 95-97.

Goodman, 1955. Correlation between cloud shade and shedding in cotton. Nature 176:39.

Guinn, G. 1974a. Abscission of cotton floral buds and bolls as influenced by factors affecting photosynthesis and respiration. Crop Sci. 14:291-293.

Guinn, G. 1974b. Abscission, ethylene evolution, and abscisic acid content of young bolls in response to low light intensity. Proceedings 28th Cotton Defoliation-Physiology Conference. 40.

Guinn, G. 1976a. Nutritional stress and ethylene evolution by young cotton bolls. Crop Sci. 16:89-91.

Guinn, G. 1976b. Water deficit and ethylene evolution by young cotton bolls. Plant Physiol. 57:403-405.

Guinn, G. 1982a. Abscisic acid and abscission of young cotton bolls in relation to water availability and boll load. Crop Sci. 22:580-583.

Guinn, G. 1982b. Causes of square and boll shedding in cotton. U. S. Dept. Agric. Tech. Bulletin No. 1672, 22 pp.

Guinn, G. 1982c. Fruit age and changes in abscisic acid content, ethylene production, and abscission rate of cotton fruits. Plant Physiol. 69:345-352.

Guinn, G. 1985a. Abscisic acid and cutout in cotton. Plant Physiol. 77:16-20.

Guinn, G. 1985b. Fruiting of cotton. III. Nutritional stress and cutout. Crop Sci. 25:981-985.

Guinn, G. 1986. Hormonal relations during reproduction. In *Cotton Physiology*, J. R. Mauney and J. McD. Stewart, eds. 113-136.

Guinn, G. and D. L. Brummett. 1987. Concentrations of abscisic acid and indoleacetic acid in cotton fruits and their abscission zones in relation to fruit retention. Plant Physiol. 83:199-202.

Guinn, G. and D. L. Brummett. 1988a. Changes in abscisic acid and indoleacetic acid before and after anthesis relative to changes in abscission rates of cotton fruiting forms. Plant Physiol. 87:629-631.

Guinn, G. and D. L. Brummett. 1988b. Changes in free and conjugated indole-3-acetic acid and abscisic acid in young cotton fruits and their abscission zones in relation to fruit retention during and after moisture stress. Plant Physiol. 86:28-31.

Guinn, G. and D. L. Brummett. 1989a. Changes in amide-linked and ester indole-3-acetic acid in cotton fruiting forms during their development. Plant Physiol. 89:941-944.

Guinn, G. and D. L. Brummett. 1989b. Fruiting of cotton. IV. Nitrogen, abscisic acid, indole-3-acetic, and cutout. Field Crops Res. 22:257-266.

Guinn, G. and D. L. Brummett. 1992. Influence of defruiting on the abscisic acid and indole-3-acetic contents of cotton leaves. Field Crops Res. 28:257-262.

Guinn, G. and J. R. Mauney. 1984a. Fruiting of cotton. I. Effects of moisture stress on flowering. Agron. J. 76:90-94.

Guinn, G. and J. R. Mauney. 1984b. Fruiting of cotton. II. Effects of plant moisture status and active boll load on boll retention. Agron. J. 76:94-98.

Guinn, G., J. R. Dunlap, and D. L. Brummett. 1990. Influence of water deficits on the abscisic acid and indole-3-acetic acid contents of cotton flower buds and flowers. Plant Physiol. 93:1117-1120.

Guinn, G., J. R. Mauney, and K. E. Fry. 1981. Irrigation scheduling and plant population effects on growth, bloom rates, boll abscission, and yield of cotton. Agron. J. 73:529-534.

Guinn, G., J. D. Hesketh, K. E. Fry, J. R. Mauney, and J. W. Radin. 1976. Evidence that photosynthesis limits yield of cotton. Proceedings 30th Cotton Physiology Conference. 60-61.

Harris, K. and R. S. Hawkins. 1942. Irrigation requirements of cotton on clay loam soils in the Salt River Valley. Arizona Agric. Exp. Sta. Bulletin No. 181.

Hearn, A. B. 1972. The growth and performance of rain-grown cotton in a tropical upland environment. 2. The relationship between yield and growth. J. Agric. Sci., Cambridge. 79:137-145.

Hearn, A. B. 1975. Responses of cotton to water and nitrogen in a tropical environment. II. Date of last watering and rate of application of nitrogen fertilizer. J. Agric. Sci. , Cambridge 84:419-430.

Heitholt, J. J. 1994a. Plant population density and cotton canopy development. Proceedings Beltwide Cotton Conferences. 1331.

Heitholt, J. J. 1994b. Supplemental boron, boll retention percentage, ovary carbohydrates, and lint yield in modern cotton genotypes. Agron. J. 86:492-497.

Heitholt, J. J. 1995. Cotton flowering and boll retention in different planting configurations and leaf shapes. Agron. J. 87:994-998.

Heitholt, J. J. and J. H. Schmidt. Receptacle and ovary assimilate concentrations and subsequent boll retention in cotton. Crop Sci. 34:125-131.

Hewitt, E. J. 1963. The essential nutrient elements: requirements and interactions in plants. In *Plant Physiology*, vol III, *Inorganic Nutrition of Plants*, F. C. Steward, ed. 137-360. Academic Press, New York.

Hinkle, D. A. and A. L. Brown. 1968. Secondary nutrients and micronutrients. In *Advances in Production and Utilization of Quality Cotton: Principles and Practices*, F. C. Elliot, M. Hoover, and W. K. Porter, Jr., eds. 281-320. Iowa State Univ. Press.

Horton, R. F. and D. J. Osborne. 1967. Senescence, abscission and cellulase activity in *Phaseolus vulgaris*. Nature (London) 214:1086-1088.

Jackson, M. B. and D. J. Osborne. 1972. Abscisic acid, auxin and ethylene in explant abscission. J. Exp. Bot. 23:849-862.

Joham, H. E. 1957. Carbohydrate distribution as affected by calcium in cotton. Plant Physiol. 32:113-117.

Joham, H. E. 1986. Effects of nutrient elements on fruiting efficiency. In *Cotton Physiology*, J. R. Mauney and J. McD. Stewart, eds. 79-90. The Cotton Foundation.

Johnson, R. E. and F. T. Addicott. 1967. Boll retention in relation to leaf and boll development in cotton (*Gossypium hirsutum* L.). Crop Sci. 7:571-574.

Jones, H. G. 1973. Moderate-term water stresses and associated changes in some photosynthetic parameters in cotton. New Phytol. 72:1095-1105.

Jones, W. R., J. D. Hesketh, E. J. Kamphrath, and H. D. Bowen. 1974. Development of a nitrogen balance for cotton growth models: a first approximation. Crop Sci. 14:541-546.

Jordan, W. R., K. W. Brown, and J. C. Thomas. 1975. Leaf age as a determinant of stomatal control of water loss from cotton during water stress. Plant Physiol. 56:595-599.

Kerby, T. A. and D. R. Buxton. 1981. Competition between adjacent fruiting forms in cotton. Agron. J. 73:867-871.

Kerby, T. A. and D. R. Buxton. 1978. Effect of leaf shape and plant population on rate of fruiting position appearance in cotton. Agron. J. 70:535-538.

King, C. C, Y. W. Tang, T. S. Ni, and others. 1956. Studies on the boll shedding of the unfertilized ovaries in cotton plant. Acta Botanique Sinica 5:77.

Kittock, D. L. 1979. Pima and upland cotton response to irrigation management. Agron. J. 71:617-619.

Krieg, D. R. 1986. Feedback control and stress effects on photosynthesis. In *Cotton Physiology*, J. R. Mauney and J. McD. Stewart, eds. 227-243. The Cotton Foundation.

Ku, S-B. and G. E. Edwards. 1977. Oxygen inhibition of photosynthesis. I. Temperature dependence and relation to O_2/CO_2 solubility ratio. Plant Physiol. 59:986-990.

Kuehl, R. O., D. R. Buxton, and R. E. Briggs. 1976. Application of time series analysis to investigate crop and environment relationships. Agron. J. 68:491-495.

Laing, W. A., W. L. Ogren, and R. H. Hageman. 1974. Regulation of soybean net photosynthetic CO_2 fixation by the interaction of CO_2, O_2, and ribulose 1,5-diphosphate carboxylase. Plant Physiol. 54:678-685.

Lancaster, J. D., B. C. Murphy, B. C. Hunt, Jr., and others. 1962. Boron now recommended for cotton. Miss. Agric. Exp. Sta. Bulletin No. 635.

Lashin, M. H., A. Raafat, and M. El Kadi. 1970. Fruiting and shedding of cotton as influenced by irrigation frequency and nitrogen level. Z. Acker. Pflanz. 131:128-136.

Lawlor, D. W. 1976. Water stress induced changes in photosynthesis, photorespiration, respiration and CO_2 compensation concentration of wheat. Photosynthetica 10:378-387.

Lawlor, D. W. and H. Fock. 1975. Photosynthesis and photorespiratory CO_2 evolution of water-stressed sunflower leaves. Planta 126:247-258.

Leigh, T. F., D. W. Grimes, W. L. Dickens, and C. E. Jackson. 1974. Planting pattern, plant population, irrigation, and insect interactions in cotton. Environ. Ent. 3:492-496.

Letham, D. S. 1967. Chemistry and physiology of kinetin-like compounds. Annu. Rev. Plant Physiol. 18:349-364.

Lewis, L. N. and J. E. Varner. 1970. Synthesis of cellulase during abscission of *Phaseolus vulgaris* leaf explants. Plant Physiol. 46:194-199.

Lipe, J. A. and P. W. Morgan. 1972. Ethylene: role in fruit abscission and dehiscence processes. Plant Physiol. 50:759-764.

Lipe, J. A. and P. W. Morgan. 1973. Ethylene, a regulator of young fruit abscission. Plant Physiol. 51:949-953.

Liu, W. C. and H. R. Carns. 1961. Isolation of abscisin, an abscission accelerating substance. Science 134:384-385.

Lloyd, F. E. 1920. Environmental changes and their effect upon boll-shedding in cotton. Annals New York Acad. Sci. 24:1-131.

Longenecker, D. E. and L. J. Erie. 1968. Irrigation water management. In *Advances in Production and Utilization of Quality Cotton: Principles and Practices.* F. C. Elliot, M. Hoover, and W. K. Porter, Jr., eds. 321-345. Iowa State Univ. Press.

Luckwill, L. C. 1954. Parthenocarpy and fruit development in relation to plant regulators. In *Plant Regulators in Agriculture,* H. B. Tukey, ed. 81-98. John Wiley and Sons, Inc., New York.

Marani, A. and D. Levi. 1973. Effect of soil moisture during early stages of development on growth and yield of cotton plants. Agron. J. 65:637-641.

Mason, T. G. 1922. Growth and abscission in Sea Island cotton. Annals of Botany 36:457-483.

Mauney, J. R. and T. J. Henneberry. 1979. Identification of damage symptoms and patterns of feeding of plant bugs in cotton. J. Econ. Entomol. 72:496-501.

Mauney, J. R. and T. J. Henneberry. 1984. Causes of square abscission in cotton in Arizona. Crop Sci. 24:1027-1030.

Mauney, J. R., G. Guinn, and K. E. Fry. 1978. Relationship of photosynthetic rate to growth and fruiting of cotton, soybean, sorghum, and sunflower. Crop Sci. Crop Sci. 18:259-263.

Mauney, J. R., T. J. Henneberry, and T. R. Russell. 1980. Soft rot of cotton squares--another cause of shed. Proceedings Beltwide Cotton Conferences. 80.

McMichael, B. L., and J. D. Hesketh. 1977. Field investigations on the response of cotton to water deficits. Proceedings 31st Cotton Physiology Conference. 62-63.

McMichael, B. L., W. R. Jordan, and R. D. Powell. 1973. Abscission processes in cotton: induction by plant water deficit. Agron. J. 65:202-204.

McNairn, R. B. 1972. Phloem translocation and heat-induced callose formation in field-grown *Gossypium hirsutum* L. Plant Physiol. 50:366-370.

McNamara, H. C., D. R. Hooton, and D. D. Porter. 1940. Differential growth rates in cotton varieties and their response to seasonal conditions in Greenville, Tex. U. S. Dept. Agric. Tech. Bulletin No. 710.

Meyer, V. 1969. Some effects of genes, cytoplasm and environment on male sterility of cotton (*Gossypium*). Crop Sci. 9:237-242.

Morgan, P. W. and J. I. Durham. 1972. Abscission: potentiating action of auxin transport inhibitors. Plant Physiol. 50:313-318.

Morgan, P. W. and J. I. Durham. 1975. Ethylene-induced leaf abscission is promoted by gibberellic acid. Plant Physiol. 55:308-311.

Morgan, P. W. and H. W. Gausman. 1966. Effects of ethylene on auxin transport. Plant Physiol. 41:45-52.

Morgan, P. W., E. Beyer, and H. W. Gausman. 1968. Ethylene effects on auxin physiology. In *Biochemistry and Physiology of Plant Growth Substances*, F. Wightman and

G. Setterfield, eds. 1255-1273. The Runge Press, Ottawa, Canada.

Morgan, P. W., C.-J. He, J. A. De Greef, and M. P. De Proft. 1990. Does water deficit stress promote ethylene synthesis by intact plants? Plant Physiol. 94:1616-1624.

Mosjidis, C. O'H., C. M. Peterson, B. Truelove, and R. R. Dute. 1993. Stimulation of pod and ovule growth of soybean, *Glycine max* (L.) Merr. by 6-benzylaminopurine. Ann. Bot. 71:193-199.

Nevins, D. J. and R. S. Loomis. 1970. Nitrogen nutrition and photosynthesis in sugar beet (*Beta vulgaris* L.). Crop Sci. 10:21-25.

Ohki, K. 1976. Effect of zinc nutrition on photosynthesis and carbonic anhydrase activity in cotton. Physiol. Plant. 38:300-304.

Ohkuma, K., F. T. Addicott, O. E. Smith, and W. E. Thiessen. 1965. The structure of abscisin II. Tetrahedron Letters. 29:2529-2535.

Ohkuma, K, J. L. Lyon, F. T. Addicott, and O. E. Smith. 1963. Abscisin II, and abscission-accelerating substance from young cotton fruit. Science 142:1592-1593.

Osborne, D. J. and S. E. Moss. 1963. Effect of kinetin on senescence and abscission in explants of *Phaseolus vulgaris*. Nature (London) 200:1299-1301.

Page, N. R. and P. J. Bergeaux. 1961. Boron status and needs of the southern region. Plant Food Rev. 7:12-17.

Patterson, L. L., D. R. Buxton, and R. E. Briggs. 1978. Fruiting in cotton as affected by controlled boll set. Agron. J. 70:118-122.

Peacock, H. A., J. T. Reid, and B. S. Hawkins. 1971. Cotton (*Gossypium hirsutum* L.) yield, stand, and bolls per plant as influenced by seed class and row width. Crop Sci. 11:743-747.

Peoples, T. R. and M. A. Matthews. 1981. Influence of boll removal on assimilate partitioning in cotton. Crop Sci. 21:283-286.

Pettigrew, W. T. 1994. Source-to-sink manipulation effects on cotton lint yield and yield components. Agron. J. 86:731-735.

Powell, R. D. 1969. Effect of temperature on boll set and development of *Gossypium hirsutum*. Cotton Grow. Rev. 46:29-36.

Presley, J. T. 1953. Verticillium wilt of cotton. In *Plant Diseases, the Yearbook of Agriculture.* A. Stefferud, ed. 301-303. U. S. Dept. of Agric., Washington, D. C.

Radin, J. W. and J. R. Mauney. 1986. The nitrogen stress syndrome. In *Cotton Physiology*, J. R. Mauney and J. McD. Stewart, eds. 91-105. The Cotton Foundation.

Ratner, A., R. Goren, and S. P. Monselise. 1969. Activity of pectin esterase and cellulase in the abscission zone of citrus leaf explants. Plant Physiol. 44:1717-1723.

Reid, P. D., F. T. Lew, and L. N. Lewis. 1971. Cellulase isozymes in *Phaseolus vulgaris* abscission zones. Plant Physiol. 47(S):42.

Riov, J. 1974. A polygalacturonase from citrus leaf explants. Role in abscission. Plant Physiol. 53:312-316.

Saad, S. I. 1951. Studies on the physiology of the cotton plant. III. Effects of shading, defoliation, and debudding on development, flowering, and shedding of the cotton plant. Proceedings Egyptian Acad. Sci. 7:59-74.

Sagee, O., R. Goren, and J. Riov. 1980. Abscission of citrus leaf explants. Interrelationships of abscisic acid, ethylene, and hydrolytic enzymes. Plant Physiol. 66:750-753.

Singh, S. P. 1975. Studies on the effects of soil moisture stress on the yield of cotton. Indian J. Plant Physiol. 18:49-55.

Skoog, F. 1940. Relationship between zinc and auxin in the growth of higher plants. Am. J. Bot. 27:939-951.

Smith, A. L. 1953. Fusarium and nematodes on cotton. In *Plant Diseases, the Yearbook of Agriculture*, A Stefferud, ed. 292-298. U. S. Dept. Agric., Washington, D. C.

Sorour, F. A. and S. F. A. Rassoul. 1974. Effect of shading at different stages of growth of the cotton plant on flowering and fruiting, boll shedding, yield of seed cotton and earliness. Libyan J. Agric. 3:39-43.

Stewart, S. D. and W. L. Sterling. 1989. Causes and temporal patterns of cotton fruit abscission. J. Econ. Ent. 82:954-959.

Stockton, J. R., L. D. Doneen, and V. T. Walhood. 1961. Boll shedding and growth of the cotton plant in relation to irrigation frequency. Agron. J. 53:272-275.

Tsui, C. 1948. The role of zinc in auxin synthesis in the tomato plant. Am. J. Bot. 35:172-179.

Tucker, M. L., S. L. Baird, and R. Sexton. 1991. Bean leaf abscission: tissue-specific accumulation of a cellulase m-RNA. Planta 186:52-57.

Tucker, M. L., R. Sexton, E. del Campillo, and L. N. Lewis. 1988. Bean abscission cellulase, characterization of a cDNA and regulation of gene expression by ethylene and auxin. Plant Physiol. 88:1257-1262.

Tucker, T. C. and B. B. Tucker. 1968. Nitrogen nutrition. In *Advances in Production and Utilization of Quality Cotton: Principles and Practices*, F. C. Elliot, M. Hoover, and W. K. Porter, Jr., eds. 185-211. Iowa State Univ. Press, Ames, Iowa.

Vaadia, Y. 1976. Plant hormones and water stress. Philosophical Transactions of the Royal Society of London. B. Biological Sciences 273:513-522.

Varma, S. K. 1976. Role of abscisic acid in the phenomena of abscission of flower buds and bolls of cotton (*Gossypium hirsutum* L.) and its reversal with other plant regulators. Biol. Plant. 18:421-428.

Vaughan, A. K. F. and G. C. Bate. 1977. Changes in the levels of ethylene, abscisic acid-like substances and total non-structural carbohydrate in young cotton bolls in relation to abscision induced by a dark period. Rhodesian J. Agric. Res. 15:51-63.

Verhalen, L. M., R. Mamaghani, W. C. Morrison, and R. W. McNew. 1975. Effect of blooming date on boll retention and fiber properties in cotton. Crop Sci. 15:47-52.

Wadleigh, C. H. 1944. Growth status of the cotton plant as influenced by the supply of nitrogen. Arkansas Agric. Exp. Sta. Bulletin No. 446, 138 pp.

Wiese, M. V. and J. E. DeVay. 1970. Growth regulator changes in cotton associated with defoliation caused by *Verticillium albo-atrum*. Plant Physiol. 45:304-309.

Zeiher, C., N. Matumba, P. Brown, and J. Silvertooth. 1995. Response of upland cotton to elevated night temperatures. II. Results of controlled environment studies. Proceedings Beltwide Cotton Conferences. 1129-1130.