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Causes of Square and Boll Shedding in Cotton

Abstract

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Cellulase and pectinase are degradative enzymes that weaken cells in the abscission zone and cause shedding of leaves and fruiting forms. Any condition that causes shedding must directly or indirectly affect the activity of these enzymes. Auxin suppresses the synthesis of the cellulase that causes abscission, whereas ethylene promotes cellulase synthesis. Abscisic acid may directly affect shedding, or it may cause an increase in ethylene. Cytokinins and gibberellins affect the movement of nutrients and indirectly affect abscission.

Environment affects square (floral bud) and boll (fruit) shedding, apparently because it affects hormonal balance. Light, temperature, drought, insects, diseases, and inorganic nutrients all affect shedding rate. Because an inadequate supply of organic nutrients increases ethylene production, conditions that decrease photosynthesis tend to increase shedding. Shedding also increases with increasing boll load, probably because of competition for nutrients.

The effects of spacing and environmental conditions are discussed in relation to hormones and square and boll shedding.

Keywords: Abscisic acid, abscission, auxin, boll, cotton, cytokinins, diseases, drought, ethylene, gibberellins, gossypium, inorganic nutrients, insects, light, shedding, spacing, square, temperature, water.

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Causes of Square and Boll Shedding in Cotton

Gene Guinn¹

Introduction

Square (floral bud) and boll (fruit) shedding have interested cotton producers and research workers for many years. More attention has been given to boll shedding than to square shedding, possibly because shed bolls are easier to see than the smaller squares. Some researchers regard shedding as a disorder that, if corrected, would greatly increase yield. Others believe that shedding is a natural process by which the plant adjusts its fruit load to match the supply of organic and inorganic nutrients. Some shedding is inevitable, especially toward the end of a fruiting cycle. Heavy shedding early in the fruiting cycle, however, can usually be attributed to specific causes, many of which can be corrected. Heavy shedding that occurs before a good crop of bolls is set is undesirable because it delays the crop and may reduce yields. With the current emphasis on short-season production to cut costs and avoid late-season insect and weather problems, a good early setting of bolls is highly desirable.

Early research workers tried to explain shedding in terms of one or a few factors. For example, Lloyd (1920)² attributed variation in shedding of squares and bolls to variations in rain and soil moisture supply. Subsequent work has clearly shown that drought increases shedding, but not all shedding can be attributed to drought.

Mason (1922) recognized the importance of photosynthesis in regulating abscission (shedding). He noted that dark, rainy weather increased shedding, and leaf removal caused almost complete shedding of young bolls. This work, according to Eaton (1955), marked the beginning of the "nutritional theory of boll shedding." According to this theory, "the cotton plant retains only as many bolls as it can supply with carbohydrates, nitrogen, or other nutrients" (Eaton 1955).

The nutritional theory was supported by the work of others and was used to explain boll shedding until the midfifties. Eaton and Rigler (1945) and Eaton and Ergle (1953, 1954), however, obtained results that could not adequately be explained in terms of 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 that is moved out into the fruiting branches." Workers subsequently concentrated on the roles of different hormones in controlling abscission.

Research by Addicott and Carns and their co-workers led to the discovery of abscisic acid (ABA) as it was later named. ABA appeared to

have most of the properties of the anti-auxin postulated by Eaton and Ergle; it was found in bolls and counteracted the growth-promoting effects of auxin (Carns et al. 1960).

Hall (1958) and his students at Texas A & M investigated ethylene as a regulator of cotton leaf and fruit abscission. Lipe and Morgan (1972, 1973) obtained convincing evidence that ethylene is a regulator of boll abscission.

Recent work has shown that nutritional status affects ethylene production by young cotton bolls (Guinn 1976a). Therefore, it appears that environmental factors influence shedding through their effects on plant hormones. The technical details of the abscission process have been presented elsewhere (Addicott 1970; Carns 1966; Guinn 1979) and will only be summarized here.

Some who work with cotton would like a simple explanation of square and boll shedding, but shedding is affected by many factors, both internal and external. In the following pages, I will attempt to explain the abscission process and show how environmental conditions interact to modify hormonal balance and enzyme activities that cause shedding.

Hormone Effects

The abscission zone, or separation layer, occurs at the base of the peduncle where it joins the fruiting branch (figs. 1 and 2). When abscission occurs, a distinct cross-sectional layer of cells becomes softened and weakened. Two enzymes are involved: (1) pectinase, which digests the middle lamella between cells; and (2) cellulase, which attacks cellulose in the cell walls. The action of these two enzymes weakens the cells in the separation layer sufficiently that bolls and large squares drop off. Small squares, however, may dry in place unless some physical force dislodges them. The cellulase is a special kind that is synthesized only when conditions favor abscission (Reid et al. 1974; Durbin et al. 1981). Any condition that causes shedding must directly or indirectly affect the synthesis, secretion, or activity of one or both of these degradative enzymes. Certain of the plant hormones regulate the synthesis, secretion, and activity of pectinase and cellulase. Hormonal balance, in turn, is influenced by environmental conditions.

Auxin (IAA) usually inhibits abscission. Treatment with IAA prevents an increase in the specific cellulase that causes abscission (Abeles 1969; Ratner et al. 1969; Lewis and Varner 1970), but it is not clear whether the effect is due to a direct inhibition of synthesis of the abscission-promoting cellulase or to indirect effects. Factors that slow the movement of IAA to the abscission zone tend to promote abscission (Morgan and Durham 1972).

Ethylene is a potent abscission-promoting hormone. Two mechanisms of action have been established: (1) slowed transport and destruction of auxin (Morgan et al. 1968; Beyer

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²The year in italic, when it follows the author's name, refers to Literature Cited, p. 13.



Figure 1.—Young cotton boll with barely visible abscission zone.

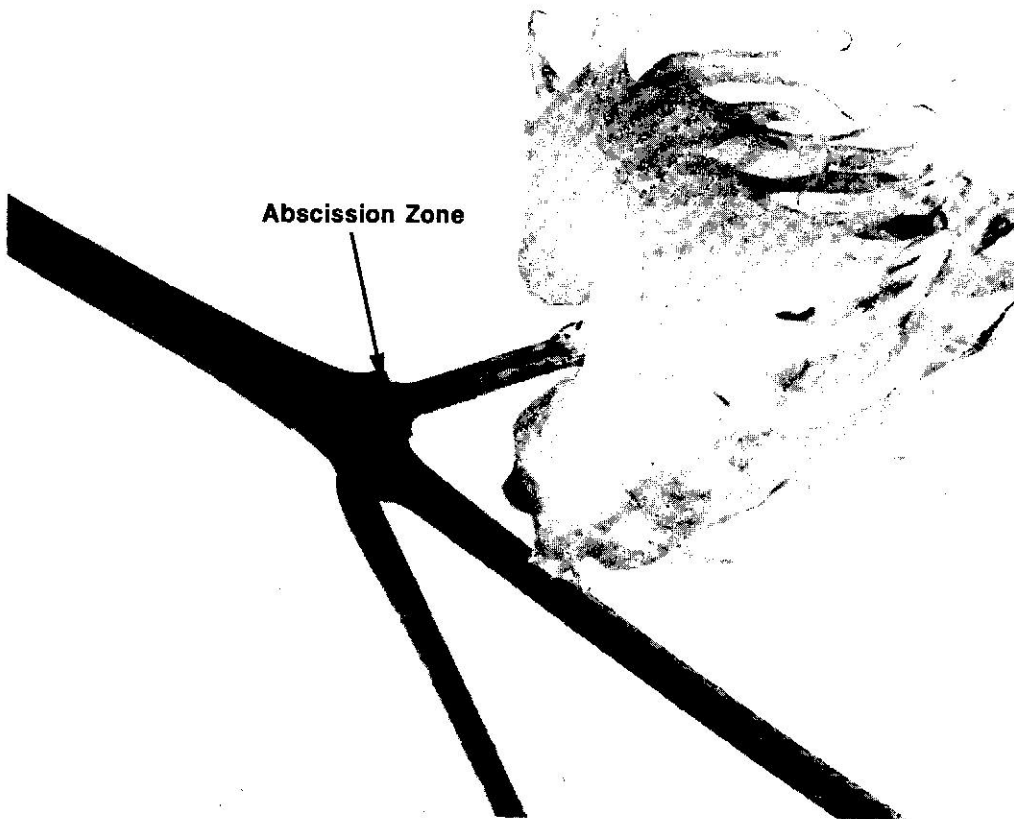


Figure 2.—Young cotton boll with well-developed abscission zone. Abscising squares and bolls develop an abnormal light yellow-green color and stop growing. The difference in diameter between the peduncle and its point of attachment to the fruiting branch is clearly evident at this late stage. Separation occurred shortly after the photograph was taken.

and Morgan 1969, 1970, 1971), and (2) stimulation of synthesis of pectinase and cellulase in the abscission zone (Rioy 1974; Horton and Osborne 1967; Abeles 1968, 1969; Ratner et al. 1969; Reid et al. 1971; Abeles et al. 1971).

The actions of ABA and ethylene are similar in many respects. The situation is complicated by the fact that ABA can stimulate ethylene production in at least some tissues (Craker and Abeles 1969; Abeles et al. 1971; Jackson and Osborne 1972; Sagee et al. 1980). Therefore, its effects could be indirect, through increased ethylene, rather than direct. Results with citrus leaves showed, rather conclusively, that ABA promoted abscission by increasing ethylene synthesis in that tissue; when ethylene synthesis was blocked with an inhibitor, ABA did not cause abscission (Sagee et al. 1980). Some evidence has been obtained, however, that ABA has direct effects that are not dependent upon increased ethylene production (Cracker and Abeles 1969; Cooper and Horanic 1973).

Gibberellic acid (GA) prevents boll shedding when applied directly to the boll (Walhood 1957; Varma 1976; Cognée 1976) but not when applied to the entire plant (Johnson and Addicott 1967). Native GA is probably important in boll retention; Rodgers (1977) found more GA in retained bolls than in bolls that were shedding, and Bhardwaj and Dua (1972) found more GA in bolls of a variety that shed few bolls than in a variety that shed many bolls.

The role of cytokinins in regulating abscission appears to be indirect. Cytokinins delay or prevent senescence and promote the ability of an organ to compete for metabolites (Letham 1967). Senescence increases the sensitivity of organs to the abscission-promoting effects of ethylene (De la Fuente and Leopold 1968; Leopold 1971). Symptoms of senescence (for example, yellowing) usually precede the shedding of squares and bolls; however, the application of cytokinins may promote rather than prevent shedding unless made directly to the abscission zone (Varma 1976; Osborne and Moss 1963).

Many native and applied substances can affect abscission, but few directly control the synthesis, secretion, and activity of pectinase and cellulase in the abscission zone. IAA, ethylene, and (possibly) ABA appear to be the hormones most directly involved. Other hormones and substances may affect abscission indirectly through their effects on growth, IAA synthesis and transport, senescence, and the synthesis of ethylene. The control of abscission does not reside in any one hormone, nutrient, or environmental factor but is regulated by the complex interaction of hormones, nutrients, and the environment.

Environmental Effects

Light

Cotton is a "sun-loving" plant and light intensity has a profound effect upon fruiting and boll shedding (Mason 1922; Goodman 1955; Dunlap 1945; Eaton and Rigler 1945; Eaton and Ergle 1953; Saad 1951; Sorour and Rassoul 1974; Guinn 1976a, 1982b; Vaughan and Bate 1977).

A period of cloudy weather can cause a temporary increase in rates of square and boll shedding (Mason 1922; Goodman

1955). If the cloudy weather is accompanied by rain, pollen may be ruptured when rain falls in the open flowers before pollination. The poorly pollinated flowers subsequently shed (Lloyd 1920; King et al. 1956) because they contain few fertilized ovules. Developing ovules probably produce IAA, gibberellins, and cytokinins (Luckwill 1954; Bhardwaj et al. 1975) that are necessary to mobilize the assimilates required for continued growth (Johnson and Addicott 1967). Even without rain, cloudy weather can cause boll shedding by decreasing photosynthesis. Some varieties are more sensitive to dim light than others. Plants with the heaviest boll loads are the most sensitive (Goodman 1955), probably because of their heavy demand for photosynthates.

Rain causes renewed growth, and the new leaves are likely to grow larger because leaf expansion is strongly influenced by leaf water potential (Boyer 1976). The resulting leafiness increases mutual shading and decreases the rate of photosynthesis by lower leaves. A loss of squares and bolls during the cloudy weather further stimulates subsequent plant growth. With the return of fair weather, photosynthate that would have gone to developing bolls, if they had not shed, becomes available for renewed plant growth.

A combination of cloudy weather with rain, excess nitrogen, and a high plant population can cause plants to become excessively vegetative. The taller plants, with most of their bolls borne on the upper part of the plant, become top heavy and tend to lodge. The exclusion of sunlight and resulting high humidity promote boll rotting, and the tangle of stems and leaves interferes with defoliation and harvesting (Peebles et al. 1956). Early setting of bolls, on the other hand, limits plant growth (Guinn et al. 1981) and results in shorter, stockier plants.

Low light intensity may affect abscission through an effect on plant hormones. The rate of photosynthesis and, therefore, the amount of carbohydrate available for growth decrease with decreasing light intensity. Organic substances, supplied by photosynthesis, are required for embryo development. Because embryos are a major source of IAA, abortion of embryos would limit the supply of IAA and abscission could result (Addicott and Lynch 1955). Factors that stimulated photosynthesis increased boll retention and, conversely, factors that increased respiration increased boll shedding (Guinn 1974a). Enrichment of the atmosphere with CO₂ was used as an experimental method for determining the effects of increased photosynthesis. This treatment increased the rate of blooming, decreased boll shedding, and markedly increased yield (Guinn 1974a; Guinn et al. 1976; Mauney et al. 1978).

Although photosynthates are necessary for the synthesis of hormones, a nutritional stress increases the production of ethylene and ABA (Guinn 1976a, 1982b; Vaughan and Bate 1977). The reasons for this apparent anomaly have not been determined, but some results suggest that loss of membrane integrity may be involved in increased ethylene production (Guinn 1977).

The evidence suggests a three-way interaction between assimilates and plant hormones. First, certain hormones, such as IAA, cytokinins, and gibberellins, can mobilize assimilates

and cause them to move to a boll in competition with other sinks. Second, assimilates are required for the continued production of these hormones. Third, the production of ethylene and ABA, hormones that promote abscission, is somehow increased by a deficiency of assimilates.

The effects of assimilate deficiency in limiting the synthesis of IAA, cytokinins, and gibberellins and in stimulating the synthesis of ethylene and ABA provide a mechanism for explaining the nutritional theory of boll abscission. 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.

Spacing

At one time, a long fruiting season was thought desirable because it permitted maximum yields; however, the increasing costs of insect control programs and the difficulty of controlling late-season insect population explosions make a shorter season desirable. Increasing costs of irrigation also add to the cost of long seasons in irrigated regions. Therefore, considerable effort has been given to developing genetic lines and cultural practices that permit a shorter growing and fruiting season.

In theory, high plant populations should promote earliness and shorten the time required to produce a crop. In some cases, high plant populations have given the expected results, but in other cases the results have been disappointing. One of the hazards is that a large percentage of the plants may become barren (Peacock et al. 1971). Eaton and Rigler (1945) noted that the combination of close spacing, fertile soils, and abundant moisture greatly decreased relative fruitfulness (the ratio of bolls to plant weight) of cotton. Nonfruitful plants were sometimes observed on rich moist soils. These nonproductive rank-growing plants were referred to variously as "he cotton," "bull cotton," and "cotton gone to weeds." Barren plants should, indeed, be considered as weeds.

The most likely cause of poor fruiting of crowded plants is low light intensity in the canopy. The effects of irradiance on photosynthesis and abscission were discussed in the previous section on light. It is difficult to discuss spacing, light, nitrogen, and water separately because they are interrelated. Spacing affects light intensity in the plant canopy. Nitrogen and water stimulate plant growth in height, number of leaves, and leaf size. Thus, adequate N and water cause greater shading of a larger percentage of the leaves. With very high plant populations, this shading may become critical in limiting photosynthesis of most of the leaves on each plant. With tall plants in high populations, only the leaves near the tops of the plants get enough light to be productive. Periods of cloudy weather intensify the problem. Lower leaves may not get enough light to support themselves and cannot contribute to boll growth and production.

Senescence and abscission of lower leaves are not uncommon on densely crowded plants. Brown (1971) noted that total fruiting positions, bolls, and buds decreased as plant popula-

tion increased, with the effect being most pronounced in the bottom third of the plant canopy and least pronounced in the top third. Shedding increased with increasing population. Gerard et al. (1976a) reported that square shedding was positively correlated with plant height in high-population plants. Gerard and Reeves (1974, 1975) and Gerard et al. (1976a, b) showed that excessive vegetative growth, which resulted from a combination of high plant population (320,000 plants/ha), irrigation or rain, excess N, and a sandy loam soil, caused marked reduction in yields. Bhardwaj et al. (1971) compared 15 varieties of upland cotton and found that the dwarf type had a higher fruiting coefficient and produced higher yields than taller types.

High plant populations may delay appearance of the first boll (Eaton 1955; Peebles et al. 1956; Brown 1971) and, thus, decrease rather than increase earliness. Gerard and Reeves (1975) reported that high density increased earliness in dry years, but delayed fruiting and decreased yields when excessive rain fell during the early part of the fruiting season. Conversely, Brown (1971) found that crowded plants shed a high percentage of their fruits during a dry year, presumably because the high plant population rapidly depleted the limited water supply.

Crowding can also decrease boll size (Bridge et al. 1973; Hawkins and Peacock 1973; Buxton et al. 1979), probably because the carbohydrate supply is inadequate in the lower portion of the plant canopy (Saleem and Buxton 1976). Cotton bolls obtain most of their photosynthate from subtending and adjacent leaves (Ashley 1972; Brown 1973; Elmore and Hacskeylo 1973; Horrocks et al. 1978). Therefore, heavy shading by upper leaves could decrease the availability of photosynthate to bolls on the lower portion of the plant and limit their growth.

Although the terms "narrow row" and "high plant population" are frequently used together, they should not be confused. Cotton grown in narrow rows does not have to be at high plant populations. At a given plant population, narrow-row culture gives a plant pattern that intercepts more sunlight early in the season, is less crowded, and produces higher yields than the same population in conventionally spaced rows (Walhood and Johnson 1976; Buxton et al. 1979). Plants in narrow rows tend to be somewhat shorter than plants in standard rows (Singh and Khan 1971; Koli and Morrill 1976; Walhood and Johnson 1976) and produce higher yields (Singh and Khan 1971; Walhood and Johnson 1976; El-Zik et al. 1977; Buxton et al. 1979). Therefore, narrow-row culture appears to be a better method for increasing productivity and shortening the growing season than high plant populations in standard rows. Unfortunately, narrow rows can create problems in mechanized cotton production: tractor tires may be too wide to pass between the rows, irrigation may be more difficult, and harvesting equipment may not be suitable. In areas where these problems do not apply, or can be overcome, the shorter season and higher yields possible with narrow-row culture make it a practice worth considering.

Position on the Plant

The location of squares and bolls has a profound effect upon their retention. The first fruiting branch typically is shorter than the next one and retains a lower percentage of squares to the

mature boll stage (Guinn, unpublished data). Retention varies even more with position on a fruiting branch; retention is high at the first node and becomes progressively lower at successive nodes out the fruiting branch. Mauney (1979) reported that 73 percent of matured bolls were borne on the first node, 24 percent at the second node, and only 2 percent at the third node. These values were obtained with irrigated upland cotton grown in Arizona under typical conditions for the area. Retention rates may vary somewhat with spacing, cultivar, and environment.

Several possible reasons for the marked difference in retention rate at different nodes on a fruiting branch can be suggested as follows:

1. Bolls obtain most of their photosynthate from subtending leaves and lesser amounts from adjacent leaves (Ashley 1972). Bolls at adjacent nodes apparently compete with each other because removal of a boll permits a greater amount of photosynthate to move from the subtending leaf to a boll at the next node (Peoples and Matthews 1981). Sink strength increases with boll age (Peoples and Matthews 1981). Bolls appear to be especially susceptible to shedding during the first week after anthesis (Guinn 1982b). Because the boll at the node closer to the main stem is about 1 week older than the boll at the next node, it is less likely to shed as a result of competition between them.

2. Fruiting branches of adjacent plants compete for space and light as they grow toward each other. Because competition increases as the branches grow, successive leaves along a fruiting branch may become more heavily shaded and, therefore, produce less photosynthate.

3. Bolls at the first fruiting branch node obtain some of their photosynthate from mainstem leaves in addition to subtending leaves (Elmore and Hacskaylo 1973; Peoples and Matthews 1981), but bolls farther out on the fruiting branch have less access to that source when a boll is present at the first node (Peoples and Matthews 1981).

4. ABA produced in bolls may move out the fruiting branch and increase the shedding rate of subsequent squares and bolls. Creelman (1975) applied radioactive mevalonolactone, a precursor of ABA, to the carpel walls of bolls at the first node and recovered the label at nodes farther out the fruiting branch. Furthermore, he found a good correlation between the amount of radioactivity and the amount of ABA measured by a different procedure (gas-liquid chromatography).

5. Nitrogen and other inorganic nutrients may be delivered in smaller amounts farther out the fruiting branch. Nitrogen, phosphorus, and other inorganic nutrients move from roots to leaves in the transpiration stream. Because bolls have relatively low transpiration rates, relatively little material moves directly to the bolls in the xylem sap (Radin and Elmore 1980). Except for calcium, which does not move in the phloem, the bulk of the inorganic ions go first to the leaves, and the portion that goes to fruits then moves from leaves to fruits in the phloem.

The accumulation of inorganic ions would be influenced by transpiration; the lower the transpiration rate in a given leaf the lower would be the movement of inorganic nutrients into

that leaf. Because of increased shading, decreased air movement, and increased humidity as the plant canopy develops above the fruiting branch, transpiration should decrease for successive leaves on a fruiting branch. Therefore, the supply of accumulated inorganic nutrients for export to developing bolls should decrease with node number on a given fruiting branch. Perhaps equally important, nitrate reduction requires a considerable amount of energy (Radin and Elmore 1980), which must be supplied, directly or indirectly, by photosynthesis. Because of lower light intensity, the rate of photosynthesis would be lower and, thus, energy for nitrate reduction could be limiting. Therefore, the supply of inorganic ions, especially reduced nitrogen, may be limited by decreased rates of transpiration and photosynthesis in leaves that develop low in the plant canopy. Much of this is speculation, however, and additional research is needed to confirm this hypothesis.

Water

Researchers have known for many years that drought can cause severe boll shedding (Ewing 1918; Lloyd 1920; and earlier papers cited therein). Ewing (1918) noted that root pruning also caused shedding, possibly because of the resulting moisture stress. Lloyd (1920) followed square and boll shedding during the entire growing season. He noted that short-term cycles were superimposed on a seasonal trend toward increased shedding, which he thought was caused by depletion of subsoil moisture. In view of later results (Goodman 1955; Johnson and Addicott 1967; Ehig and LeMert 1973), it seems more likely that the seasonal increase in shedding was caused by increasing boll load. Hawkins et al. (1933) reported that drought caused extremely slow growth and the formation of small thick-walled cells. In addition, drought increased the carbohydrate content of stems and caused lower nitrogen content and near 100 percent abscission of young bolls. McNamara et al. (1940) found that young bolls shed as soil moisture was depleted and a strong tendency existed for the squares to flower and then shed as young bolls, rather than for the large squares to shed. This observation agreed with that of Ewing (1918) who noted that, apart from insect damage, shedding of squares was rare and shedding of open flowers was extremely rare. Most shedding occurred in the young boll stage.

The timing, duration, and intensity of drought are important. A moderate stress early in the season may sometimes be beneficial. A preflowering stress has sometimes been observed to increase subsequent rate of blooming (Singh 1975; Mauney et al. 1980) and yield (Singh 1975; El-Zik et al. 1977). These results appear to conflict with research results reviewed by Longenecker and Erie (1968), which indicate that a good early season growth is essential for maximum yields.

Research results in California (Leigh et al. 1970, 1974) and Arizona (Mauney et al. 1980) indicate that plant bugs, such as *Lygus hesperus* Knight, may preferentially feed in succulent cotton and avoid stressed cotton. If this is true, a higher percentage of the squares would develop into flowers on moderately stressed than on well-watered cotton in years when plant bugs are a problem.

Water deficit apparently does not cause major square shedding early in the season before flowering (Bruce and Rom-

kens 1965; Mauney et al. 1980), but can increase square shedding after flowering starts (McNamara et al. 1940; Grimes et al. 1970; McMichael and Guinn 1980). Square shedding becomes very sensitive to drought 5 weeks after first bloom (Bruce and Romkens 1965), possibly because of the greater boll load at that time than earlier. Stress that develops after flowering begins is almost always detrimental (Longenecker and Erie 1968; Grimes et al. 1970; Guinn et al. 1981), although there are apparent exceptions (Longenecker and Erie 1968).

Drought can affect fruiting and boll abscission in several ways. Water deficit decreases photosynthesis by decreasing leaf size and, thus, photosynthetic area (Boyer 1973; Marani and Levi 1973), by causing stomatal closure (Jordan, et al. 1975; Boyer 1976; Cutler and Rains 1977; McMichael and Hesketh 1977), by decreasing the synthesis and activity of photosynthetic enzymes (Jones 1973); by decreasing photo-phosphorylation (Boyer 1973; Vieira da Silva 1973) and Hill reaction activity (Fry 1970; Vieira da Silva 1973), and by increasing photorespiration (Lawlor and Fock 1975; Lawlor 1976). Other effects of prolonged stress can also limit photosynthesis. For example, leaves may become senescent and abscise (McMichael et al. 1973), possibly as a result of decreased uptake of nitrate (Shaner and Boyer 1976) and phosphate (Greenway et al. 1969); decreased nitrate reductase activity (Shaner and Boyer 1976; Ackerson et al. 1977); increased IAA oxidase activity (Darbyshire 1971); decreased cytokinin content (Vaadia 1976); increased ethylene production (McMichael et al. 1972); increased ribonuclease activity (Marin and Vieira da Silva 1972; Arad et al. 1973); decreased polyribosome content (Boyer 1973; Vieira da Silva et al. 1974); and decreased protein synthesis (Boyer 1973; Dhindsa and Cleland 1975; Dhindsa 1976).

Drought may also decrease translocation of assimilates (McNaim 1972; Hsiao 1973; Sung and Krieg 1979; Ackerson and Herbert 1981), but photosynthesis is affected more than translocation in cotton (Sung and Krieg 1979; Ackerson and Hebert 1981). Translocation in adapted plants was not decreased when plants were stressed to a leaf water potential of -24 bars (Ackerson and Hebert 1981).

In addition to the effects of decreased photosynthesis in limiting the amount of assimilate available for boll growth, a water deficit can alter the hormonal balance in bolls. Loss of water causes bolls to produce increasing amounts of ethylene, both when plants are stressed and when detached bolls are subjected to partial desiccation (Guinn 1976b). Further, the ABA content of young bolls on field-grown plants increases as stress develops between irrigations, and the increase in ABA content parallels an increase in rate of boll shedding (Guinn 1982a). Thus, both abscission-promoting hormones (ethylene and ABA) increase with increasing stress.

Water deficit may also affect boll abscission through an effect on IAA transport to the abscission zone. Davenport et al. (1977) determined that water stress reduced the basipetal transport (movement toward the stem) of IAA in petioles of cotton cotyledons. This could be an ethylene effect because water deficit increases ethylene production in cotton petioles (McMichael et al. 1972) and ethylene decreases IAA transport (Morgan and Gausman 1966; Beyer and Morgan 1969).

Work by Morgan et al. (1977), however, indicates that water deficit decreases IAA transport more than it promotes ethylene synthesis in cotton leaves and petioles. Whether these results can be extrapolated from leaves to bolls remains to be determined.

Boll shedding in response to drought may be a mechanism that helps the plant survive and continue to grow during periods of drought. Various parts of the plant act as sinks that compete with each other for available assimilates. Different cultivars apparently differ in the competitive advantage of their bolls versus other parts of the plant (Guinn, unpublished data). Determinate cultivars produce bolls early and rapidly until the developing boll load causes a temporary cessation of growth and fruiting, commonly referred to as cut-out (Patterson et al. 1978). Bolls compete with roots for assimilates and restrict root growth. Eaton and Joham (1944) found that defruiting causes large increases in sugar content and growth of cotton roots. When root growth is restricted, water absorption by plants becomes more dependent on flow of water through the soil to the root. The movement of water through unsaturated soil, however, is very slow and, unless the roots can grow into new areas of soil, the plants will not be able to obtain enough water to prevent stress (Begg and Turner 1976).

Furthermore, the mechanical resistance of drying soil is greater than that of wet soil. The pressure potential must be adequate to permit root growth into the resistant soil, and solutes provide the major portion of the pressure potential (Hsiao 1973; Hsiao et al. 1976). Regardless of whether the osmotic solutes are sugars, organic acids, or other organic compounds, photosynthesis is the ultimate source. To the extent that developing bolls compete with roots for assimilates, the ability of roots to grow in a drying soil will be decreased. This relationship may well explain the results that caused Quisenberry and Roark (1976) to conclude that cotton cultivars with relatively indeterminate growth habit are better adapted in an environment with seasonally limited soil moisture than are cultivars with determinate growth habit. Because of their smaller boll load and less competition by bolls for available assimilates, the roots of indeterminate cultivars are probably able to grow more and extract water from a greater volume of soil than are roots of determinate cultivars.

If this line of reasoning is valid, it suggests that application of growth regulators to prevent boll abscission, or genetic selection for high bloom rate and high boll retention, may be counterproductive for plants grown under temporary drought conditions. Limited root growth of plants with a heavy boll load could cause the water stress to become so severe that photosynthesis would be severely restricted. Because of decreased photosynthesis and early termination of growth and fruiting, plants that retain most of their bolls may produce smaller bolls and produce bolls during a shorter time than plants that partition more of their available assimilate into root growth. Therefore, the yield of determinate plants may be less than that of indeterminate plants when temporary periods of water deficit occur during flowering and boll development. Conversely, determinate plants may produce more than indeterminate plants when the season is cut short by an extended drought in late summer or by cold weather early in the fall. The time during which drought occurs and expected length of

the growing season are important factors to consider in selecting an early versus a less determinate cultivar.

Too much water can also be detrimental and can cause shedding because of inadequate aeration in heavy soils or leaching of nutrients in sandy soils (Longenecker and Erie 1968), and by promoting excessive vegetative growth, especially in combination with high nitrogen fertility, high plant population, and cloudy weather (Gerard and Reeves 1974). The mutual shading by tall, leafy, crowded plants can cause shedding (see previous sections on light and spacing.)

Sprinkler irrigation or rain in open flowers can increase boll shedding by preventing pollination, as mentioned earlier.

Heavy rain or flood irrigation may cause shedding by depriving roots of oxygen. Bradford and Yang (1980) reported that an intermediate in the conversion of methionine to ethylene accumulates in tomato roots when they are flooded. The steps from methionine to 1-aminocyclopropane-1-carboxylic acid (ACC) do not require oxygen, but the conversion of ACC to ethylene does require oxygen. Therefore, ACC accumulated in waterlogged roots, moved to the tops (where there was plenty of oxygen), and was converted to ethylene (a potent abscission-promoting hormone). Perhaps the same thing happens in cotton. We observed heavy shedding after an irrigation in July when the weather was hot, the plants were fruiting heavily, and the water stood for some time (unpublished).

Three reports (McMichael et al. 1973; Hsiao 1973; Osborne 1974) indicate that bolls are retained until stress is relieved by rewatering, but all three are based on the results of McMichael et al. (1973). Most of our observations indicate that bolls can shed during a dry period and are not necessarily retained until the stress is relieved by irrigation. McMichael et al. (1973) grew their plants in pots rather than in the field. Even though they attempted to stress the plants slowly, the results may not be the same as those observed in the field where the soil dries gradually. Two other factors could cause workers to conclude that bolls are retained until the stress is relieved. (1) Stress increases with time and is most severe just before irrigation (or rain) and, therefore, the stimulus for abscission reaches a maximum at that time; and (2) a few days are required after the stimulus before the bolls actually drop (Stockton et al. 1961; Guinn 1982b).

Bolls that develop from flowers that appear on the day of irrigation, and sometimes the day before, show a much higher retention rate than those that develop from flowers that appear 2 or more days before irrigation. Stockton, Doneen, and Walhood (1961) concluded that abscission is reversible during the first 3 days after anthesis but then becomes irreversible. Another interpretation is that large squares and flowers are less likely to shed than young bolls (McNamara et al. 1940). The boll shedding rate usually decreased sharply as soon as the plants were irrigated.

Temperature

Compared with most C_3 plants, cotton is fairly heat tolerant. Excessively high temperatures can cause squares and bolls to abscise and decrease yield (Dunlap 1945; Powell 1969;

Bhatt et al. 1972; Fisher 1973; Guinn 1974a; Kuehl et al. 1976; Bhatt and Nathan 1977). High temperatures can prevent the production of viable pollen (Meyer 1969; Powell 1969; Fisher 1975), may induce callose formation in phloem and thereby decrease translocation (McNairn 1972), or may increase dark respiration (Guinn 1974a) and photorespiration (Laing et al. 1974; Ku and Edwards 1977) and thereby decrease net photosynthesis (Baker 1965).

There appears to be some difference of opinion as to the effects of high temperatures on boll setting, perhaps because of differences in cultivars and in the way the experiments were conducted. Powell (1969) grew plants in a greenhouse and transferred them to growth chambers for his temperature tests. A constant night temperature of 29.4°C caused failure of blooms to produce viable pollen; at 32.2°C the plants would not set fruit even when pollinated with viable pollen from other plants. In a field test, Ehlig and LeMert (1973), however, could find no apparent relationship between boll retention and maximum or minimum temperatures. They found, rather, that boll shedding increased as boll load increased. If they delayed boll loading by removing flowers, they also delayed the decrease in boll retention. The longer flowers were removed the later the plants retained a high percentage of their bolls after deflowering was stopped. They concluded that boll load, rather than high temperature, was the primary cause of low boll retention and cessation of flowering. Patterson et al. (1978) obtained similar results in Arizona. Rather than removing all flowers until a given date, they removed flowers through the season, leaving one flower per plant every 2, 3, 4, or 5 days. Partial defloration limited the rate of boll loading and caused plants to retain most of their bolls during August when the average temperature for the month was 33.2°C.

It may appear that the grower would have no control over boll shedding induced by high temperature, but this is not necessarily the case. The grower can exert some control over temperature by irrigation because transpiring plants cool themselves by evaporation. The leaf and canopy temperatures of drought-stressed plants can exceed those of plants with adequate water by several degrees when air humidity is low (Palmer 1967, Ehler 1973). The grower can partially overcome the adverse effects of high temperature on net photosynthesis by spacing the plants so that most of the leaves are adequately illuminated. Irrigation may also increase photosynthesis by relieving drought stress. Adequate fertilization is also necessary for maximum rates of photosynthesis (see later sections on inorganic nutrients). Finally, cultivars appear to differ in their heat tolerance (Feaster and Turcotte 1965; Feaster et al. 1967; Fisher 1975). Therefore, the grower can minimize boll shedding where high temperature occurs by (1) selecting a heat-tolerant cultivar, (2) applying an adequate amount of a balanced fertilizer, (3) planting or thinning for optimal plant spacing, and (4) irrigating as needed to prevent drought stress and maintain transpiration for evaporative cooling.

Low temperatures, on the other hand, slow boll development but do not increase boll shedding (Gipson and Joham 1968).

Insects

Insect feeding can cause serious losses of yield by interfering with plant growth, by causing leaf malformations or abscis-

sion, by increasing the shedding of squares and bolls, by damaging the seed and lint, or by a combination of these. The stimulus for square and boll shedding may be either direct (feeding on the square or boll) or indirect (withdrawing nutrients from leaves, petioles, or stems; or by causing loss of leaf area due to malformation or abscission). Much of the information in this section was obtained from the review by Gaines (1957), from discussions with L. A. Bariola, and from my personal experience.

Thrips, *Frankliniella* spp., may kill seedling plants or delay fruiting by causing stunting and leaf malformations, but they do not normally affect square or boll abscission. Other early season insects may continue feeding long enough to cause abscission of squares and bolls. The cotton fleahopper, *Pseudatomoscelis seriatus* (Reuter), causes shedding of small squares and a reduction in the number of fruiting branches. Powell and Duffey (1976) reported that fleahopper damage increased the rate of ethylene evolution. The fleahopper itself did not produce ethylene, but they were able to isolate fungi and bacteria from the damaged buds that stimulated ethylene evolution when inoculated into other buds. They concluded that fleahopper feeding inoculated the plants with fungi and bacteria that stimulated ethylene evolution, and that the ethylene was the cause of the increased square shedding.

Lygus spp. also feed on squares and cause them to abort or shed. It is difficult to determine whether small squares have been damaged by lygus bugs without resorting to microscopic examination (Mauney and Henneberry 1978). This lack of obvious visible injury may be a major reason for the differences of opinion concerning the relative importance of lygus feeding versus physiological factors in causing young squares to abscise.

As pointed out in previous sections, a high percentage of plants may be barren when adequate-to-excessive supplies of water and nitrogen are combined with high plant populations. The results of Leigh et al. (1974) suggest the interesting possibility that leaf area index (LAI) affects the populations of various plant bugs, including *Lygus hesperus* Knight. They reported that populations of *L. hesperus*, *Geocoris* spp., and *Orius tristicolor* (White) increased exponentially as LAI increase. They used irrigation and plant population to modify LAI. On the basis of their results, a higher population of plant bugs may be a factor in causing poor fruiting of crowded plants that receive adequate amounts of water and nitrogen. Differential feeding by plant bugs may also be the cause of higher initial blooming rates and higher yields reported in some drought-stressed cotton (Singh 1975; El-Zik et al. 1977; Mauney et al. 1980) because the plant bugs may preferentially feed on nonstressed plants.

Boll weevils, *Anthonomus grandis* Boheman, normally feed on squares, but will also feed on young bolls when weevil populations are large in relation to number of squares available. The females oviposit in squares and young bolls, causing the bracts to flare and the squares and young bolls to turn yellow and abscise. These symptoms are caused by the second and third instar larvae (Coakley et al. 1969). King and Lane (1969) extracted protein from boll weevil larvae that

caused the same symptoms when injected into the square, that is, flaring of bracts and abscission of the square. In subsequent papers, King (1972, 1973) reported evidence that pectinase in the protein might be involved. He concluded that growth regulator imbalances and degradation products resulting from the action of endopolymethylgalacturonase are probably the ultimate causal agents of abscission.

The cotton bollworm, *Heliothis zea* (Boddie), and the tobacco budworm, *H. virescens* (Fabricius), deposit their eggs on young leaves or growing points. After hatching, the young worms start feeding on young tissues and progress from squares to young bolls to older bolls as they grow and move down the plant. Their feeding stimulates ethylene production (Guinn, unpublished), and the ethylene is probably the hormonal signal that triggers shedding of the damaged squares and bolls.

The pink bollworm moth, *Pectinophora gossypiella* (Saunders), feeds on plant nectar and oviposits on the surface of squares or bolls or on foliage. Upon hatching, the young larvae seek bolls to enter, in which they feed and develop. In early season, before bolls are available, the larvae will enter and feed in squares. They normally feed on the immature pollen and anthers. This feeding rarely causes squares to abscise; however, if the larvae feed on the stigma of squares, or on the ovule of young bolls, the young boll will abscise soon after anthesis. Few larvae enter bolls less than 10 days old, and those that do usually do not survive. Larval feeding within older bolls rarely causes boll shedding unless several larvae are in one boll. Bolls damaged by larval feeding are subject to fungal infection, and the combination of damage from larval feeding and fungal disease may cause abscission. Even though many infested bolls remain on the plant, they are heavily damaged and are of little value (Fry et al. 1978).

Leaf feeding insects, such as the cotton leafperforator, *Bucculatrix thurberiella* Busck, the cotton leafworm, *Alabama argillacea* (Hübner), the cabbage looper, *Trichoplusia ni* (Hübner), the salt-marsh caterpillar, *Estigmene acrea* (Drury), the beet armyworm, *Spodoptera exigua* (Hübner), and the yellow-striped armyworm, *Spodoptera ornithogalli* (Guenee), can stimulate shedding by destroying much of the photosynthetic tissue and, thereby, causing a deficit of organic material for square and boll development. Spider mites, *Tetranychus* spp., cause leaf abscission and resulting losses in photosynthesis and yield.

Diseases

Diseases, as well as insects, can cause large reductions in yields. Loss of bolls may result from loss of leaves and subsequent shedding of bolls or from infection and shedding or rotting of bolls.

Verticillium wilt, caused by *Verticillium albo-atrum* (Reinke and Berth.), is a disease in which the xylem becomes partially obstructed by the fungus. Infected leaves develop chlorotic areas that gradually become larger and paler. The leaves wilt, and severely affected plants shed all their leaves and most of their bolls (Presley 1953). Wiese and DeVay (1970) investigated the effects of two isolates of the organism on hormonal

changes in cotton leaves and stems. Infection with T9, the defoliating isolate, doubled the ABA content of leaves and caused a fivefold increase in ethylene production. They did not investigate possible hormonal changes in bolls. The fungus does not need to grow in or on bolls to cause their abscission. Either a deficit of water or organic nutrients can increase ethylene evolution from bolls (Guinn 1976a, b) and cause their abscission (McMichael et al. 1973; Guinn 1974a). The fungus causes (1) water deficit by blocking the xylem and (2) a lack of organic nutrients by causing defoliation. When the leaves fall from the plant, photosynthesis is no longer possible and the bolls starve.

Fusarium wilt, caused by *Fusarium oxysporum* Schlecht. f. *vas-infectum* (Atk.) Snyd. and Hans., exhibits symptoms similar to those caused by verticillium wilt. Infected plants are stunted, and leaves wilt, turn yellow, and abscise. Bolls that do not abscise are small and contain poor quality lint (Smith 1953a). The wilting and loss of leaves should cause young bolls to abscise because of water stress and lack of organic nutrients.

The leaf spots caused by *Alternaria tenuis* Nees and *Ascochyta gossypii* Woron. can cause leaf abscission and resulting starvation of young bolls. A plant infected with *A. gossypii* may be reduced to almost bare stems with a few small leaves at the tip, or may die (Blank 1953).

Bacterial blight, *Xanthomonas malvacearum* (E. F. Sm.) Dows., can cause severe losses through reduction in stand, defoliation, shedding of small bolls, rotting of older bolls, and reduction in grade from lint staining (Blank 1953; Smith 1953b). Fortunately, resistant and immune varieties have been developed (Brinkerhoff 1970).

Anthraxnose boll rot is caused by *Glomerella gossypii* (South.) and is characterized by small, round, water-soaked spots, which enlarge and become sunken and brownish (Smith 1953b). Close spacing and humid conditions increase the severity of the boll rots. Conversely, low populations and wide spacing increase the severity of verticillium wilt (Minton et al. 1972).

Inorganic Nutrients

A deficiency of a nutrient element can increase abscission (Addicott and Lyon 1973). The roles of the essential elements are so extensive that a comprehensive discussion of their functions is beyond the scope of this review. The reader is referred to Hewitt (1963) and to Bonner and Varner (1976) for additional details.

Nitrogen

Despite possible adverse effects of excessive nitrogen (N) in promoting leafiness and vegetative growth, yield of cotton is probably more often limited by a deficiency than by an excess of N. Cotton requires relatively large amounts of N (relative to requirements for other fertilizer elements) for maximum yield. Although lint contains almost no N, the seeds contain large amounts. According to Tharp (1960), the seeds of one bale of cotton contain about 16 kg of N. Tucker and Tucker (1968) stated that the total N content of cotton plants, including the

seeds, ranges from 27 to 45 kg per bale produced. Unlike potassium and phosphate, nitrate is not fixed in the soil and, therefore, leaches readily from the root zone. The ammonium form is held by the cation exchange capacity of soils, but it is rapidly oxidized to nitrate by soil micro-organisms. Organic matter provides the only lasting form of N in soil, but in warm areas where cotton is grown, many soils have been largely depleted of organic matter. Therefore, for maximum yields, most soils require annual fertilization with some form of N.

Nitrogen has many roles in plants that affect growth and development. Nitrogen occurs in nucleic acids, all enzymes, most coenzymes, chlorophyll, auxins, cytokinins, and membrane proteins. The essential functions of N are so basic and varied that a chronic N deficiency may mask the promotion of boll abscission because so few flowers are produced. A statement of percentage of bolls shed has little meaning unless accompanied by a statement of number of flowers produced. For example, Reddy and Rao (1970) obtained the greatest number of bolls per plant and the highest yield with the highest rates of N despite a high rate of boll shedding. Crowther (1934) found the lowest rate of boll shedding with medium rates of N and medium irrigation, but he obtained the highest yield with the heaviest rates of N and irrigation; low rates of N greatly depressed flower production compared with the higher rates.

N deficiency can stimulate abscission (Addicott and Lynch, 1955; Addicott and Lyon 1973). N is a component of IAA, which inhibits abscission, and of cytokinins, which mobilize nutrients to developing bolls and thereby help prevent senescence. N deficiency may increase the ABA content of leaves (Goldbach et al. 1975; Radin and Ackerson 1981). Radin and Ackerson (1981) found that N deficiency increased ABA and caused the stomata of greenhouse-grown cotton leaves to close at a higher leaf water potential (before stress became severe) than that required to cause stomatal closure in N-sufficient plants. If the same effect occurs in field-grown cotton, deficiencies of N and water could interact. N deficiency could limit photosynthesis, in part, by inducing stomatal closure sooner during a dry period. This would conserve water, but would also limit photosynthesis, growth, and fruiting. Possible effects of N deficiency on ABA content of squares and bolls have not been determined and should be investigated.

N is essential for photosynthesis (Nevins and Loomis 1970) because it is a component of chlorophyll, enzymes, and membranes. Thus, a N deficiency would limit photosynthesis regardless of whether it induced stomatal closure.

A deficiency of N limits both the rate and the duration of flowering (Tucker and Tucker 1968; Hearn 1975) and may be a major factor in cutout of cotton. Soil N is depleted as the season progresses. Crowther (1934) obtained evidence that N uptake ceased when the plants set a load of bolls even though the soil still contained N. He suggested that root growth stopped because of competition by bolls for carbohydrates and that the cessation of root growth stopped N uptake. Whether the cessation of apical growth is caused by a N deficiency, a carbohydrate deficiency, a hormonal signal from developing bolls, or a combination of factors has not been established with certainty. N supply is considered to be

an important factor controlling new growth and abscission of squares, bolls, and leaves (Jones et al. 1974; G. C. Bate, personal communication).

Cases in which excess N increases abscission of squares and bolls and decreases yields usually involve other factors that increase the shading problem caused by vigorous plant growth. For example, Gerard and Reeves (1975) reported that application of N increased yields with plant populations of 60,000 plants per ha, but depressed yields with plant populations of 320,000 plants per ha. The results of Gerard et al. (1976a, b) provide a good example of the effects of a particularly adverse combination of factors. They planted cotton to a stand of 300,000 plants per ha (a high population) at Weslaco, Tex., on a sandy loam soil that supported vigorous plant growth.

Weslaco is near the southern tip of Texas where cloudy weather is common, and nights are humid and quite warm. On the sandy loam soil, plants sometimes grew to a height of 2 m (6 ft). Yields were inversely related to leaf N and were improved by a winter crop that removed over half the soil N before cotton was planted. Rainfall and irrigation depressed yields, which were inversely related to plant height on the sandy loam soil. It seems highly probable that a carbohydrate deficiency was induced in these plants by heavy shading in a high population of tall plants. The majority of the leaves must have been shaded so that they were unable to contribute much to total photosynthesis.

Periods of cloudy weather further restricted photosynthesis and warm nights probably depleted carbohydrates through high rates of respiration. The relatively short summer photo-periods at that southern latitude may also have been a factor in restricting photosynthesis.

Potassium

Although little, if anything, has been written about a possible effect of potassium (K) on boll abscission, the roles of K suggest that it should affect abscission; it certainly affects yield (Kamprath and Welch 1968). A deficiency of K decreases protein synthesis and increases protein degradation (Kamprath and Welch 1968; Trewavas 1972), decreases photosynthesis (Terry and Ulrich 1973; Koch and Estes 1975), increases respiration rate (Kamprath and Welch 1968), and decreases translocation (Haeder et al. 1973). K plays an important role in stomatal opening (Raschke 1975), and this role, plus its role in protein synthesis, could explain the effects of K deficiency on photosynthesis. Considering the effects of K deficiency on protein synthesis and photosynthesis and the apparent effects of N and carbohydrate deficiencies on abscission, it would be surprising if a K deficiency has no effect on boll abscission.

Calcium

Addicott and Lynch (1955) and Addicott and Lyon (1973) listed calcium (Ca) deficiency as a cause of abscission and suggested the role of Ca in the middle lamella (Ca pectates) as a possible reason. Joham (1957) found that a severe Ca deficiency caused complete failure of cotton to set bolls. A

likely reason was that Ca deficiency affected translocation of carbohydrates; a Ca deficiency caused carbohydrates to accumulate in leaves as they declined in stems and roots. Young bolls probably abscised because of starvation. A Ca deficiency may also decrease the basipetal transport of auxin (De la Fuente and Leopold 1973). Because a supply of auxin at the abscission zone inhibits abscission, interference with transport could promote abscission. Poovaiah and Leopold (1973a) reported that Ca also deferred leaf senescence, presumably because of its role in membranes. They (Poovaiah and Leopold 1973b) found that Ca inhibited abscission of bean petiole explants, and they postulated that Ca may act on stage I or the "Juvenile" stage and inhibit abscission because it is a component of the middle lamella, promotes translocation of sugars and auxin, and helps prevent senescence.

Boron

A deficiency of boron (B) causes abscission of squares and bolls (Eaton 1932; Page and Bergeaux 1961; Lancaster et al. 1962; Hinkle and Brown 1968). Eaton (1955) suggested that one reason a B deficiency causes abscission of fruits is because of its effect on translocation of sugars. In this respect, B is similar to Ca; both are needed to maintain phloem in a healthy condition. Eaton (1932) found that cotton had a higher B requirement than any of 59 other plants tested. 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). Because B is a micronutrient, large increases in yield may be obtained with the addition of small amounts to B-deficient soils (Hinkle and Brown 1968).

Zinc

Zinc (Zn) deficiency may increase abscission because Zn is required for IAA synthesis (Skoog 1940; Tsui 1948) and photosynthesis (Ohki 1976). Work by Skoog (1940) indicated that Zn-deficient tissue destroyed IAA faster than normal tissue. Later work by Tsui (1948) indicated that Zn is also required for IAA production, probably because it is required for tryptophan synthesis. Because IAA is the major hormone that inhibits abscission, a Zn deficiency should promote abscission. Furthermore, the important role of photosynthesis in maintaining boll growth and preventing abscission may provide another explanation for the effects of Zn deficiency on boll set. Zn is a component of carbonic anhydrase, and some scientists think this enzyme plays a role in photosynthesis, but not all scientists agree that it plays a significant role. Regardless of the role of carbonic anhydrase, Zn deficiency limits photosynthesis per unit of leaf area (Ohki 1976), and also causes leaves to be smaller (Hewitt 1963).

Other Nutrients

Addicott and Lyon (1973) stated that deficiencies of N, phosphorus (P), K, sulfur (S), Ca, Mg, Zn, B, and iron (Fe) increase abscission. I was unable to find reports that specifically indicate effects of P, S, Mg, or Fe deficiencies on square and boll abscission; however, a consideration of their roles in plants suggests that they should affect square and boll abscission.

A deficiency of P delays and reduces fruiting (Jones and Bardsley 1968), but it is not clear whether this is due solely to a decreased rate of plant growth and development or whether square and boll abscission may also be involved. P has many essential roles in plants; it occurs in membranes in the form of phospholipids, it is a component of the nucleic acids which are necessary for protein synthesis, and it occurs in coenzymes involved in energy transfer reactions. Energy is trapped in photosynthesis in the form of adenosine triphosphate (ATP) and reduced nicotinamide adenine dinucleotide phosphate (NADPH). This energy is then used in the photosynthetic fixation of CO₂ and the synthesis of sugars, amino acids, proteins, lipids, and other organic compounds. Most sugars are metabolized and interconverted as sugar phosphates. When sugars are respired in mitochondria, the energy is converted to ATP. The roles of P in photosynthesis, respiration, and the synthesis of nucleic acids, proteins, lipids, and other essential compounds are so basic that growth reductions may mask any abscission-promoting effects of a P deficiency.

S also has many essential roles in plants. A deficiency of S slows photosynthesis (Terry 1976), perhaps because it is necessary for chlorophyll synthesis and occurs in ferredoxin, an iron-containing protein involved in the transfer of electrons. S also occurs in two vitamins, thiamine and biotin, and in the coenzymes thiamine pyrophosphate, coenzyme A, and lipoic acid. These coenzymes are necessary for carbohydrate and lipid metabolism. S occurs in the amino acids cysteine, cystine, and methionine and, therefore, is necessary for protein synthesis. S deficiency causes protein content to decrease as soluble N fractions increase (Hewitt 1963). Because of its roles in lipid and protein synthesis, a S deficiency is likely to limit the synthesis and repair of membranes. Loss of membrane integrity could cause increased ethylene synthesis (Osborne et al. 1972; Guinn 1977), which would promote abscission.

Mg is the central atom in the ring structure of the chlorophyll molecule and, therefore, is essential for photosynthesis. It also catalyzes reactions involving ATP and, therefore, is necessary for transfer of the energy contained in high-energy phosphate bonds. In this role, it is essential in carbohydrate metabolism and the synthesis of all kinds of organic compounds such as nucleic acids, proteins, and lipids. A deficiency can cause abscission of older leaves and greatly decrease yields of fiber and seed (Hinkle and Brown 1968).

Fe is required for chlorophyll synthesis, although it is not a part of the completed molecule. A deficiency can cause extreme chlorosis. Fe is a component of ferredoxin and cytochromes, which are essential for electron transfers in photosynthesis. In addition, some of the cytochromes are necessary for electron transfers in respiration. Therefore, Fe is absolutely essential for both photosynthesis and respiration. It is not surprising that a deficiency decreases yields (Hinkle and Brown 1968).

Nutrient deficiencies may cause a decrease in growth with a concomitant reduction in the number of squares produced, they may cause an increase in abscission of fruiting forms, or they may cause both. Perhaps a key factor is the rapidity with

which the deficiency develops. A chronic deficiency may decrease growth and fruiting, whereas a rapidly developing deficiency may cause an increase in abscission. In either case, the end result will be a decrease in yield.

Seasonal Changes

Rate of boll abscission increases from the beginning to the end of the season (Lloyd 1920; Davis and Addicott 1972; Ehlig and LeMert 1973; Verhalen et al. 1975; Patterson et al. 1978). Sometimes, the decline in the percentage of bolls retained was almost linear from about 80 percent at the beginning of the season to less than ten percent at the end of the season (Verhalen et al. 1975). Lloyd (1920) suggested that the seasonal increase in boll shedding was caused by depletion of subsoil moisture. McNamara et al. (1940) also emphasized the importance of increasing water deficit in causing increasing loss of bolls. There can be little doubt that a water deficit causes increased rates of boll abscission (see section on water), but drought alone cannot explain all cases of increasing boll abscission as the season progresses.

A change in hormonal relationships is probably a factor. According to Ewing (1918), W. L. Balls ascribed the cessation of growth and flowering to senescence due to self-poisoning. Davis and Addicott (1972) measured the amount of ABA in various aged bolls of two cultivars early and late during a growing season. Abscised bolls contained much higher concentrations of ABA than retained bolls late in the fruiting season when rate of boll shedding was high. Guinn (1976a) found that rate of ethylene production by young cotton bolls increased from low values at the beginning to high values near the end of the fruiting season. Cyclic changes during irrigation cycles were superimposed upon the seasonal increase, indicating a response of ethylene production to water deficit. ABA content of young bolls also increased between irrigations (Guinn 1982a). In general, boll shedding rates paralleled the changes in ethylene evolution (Guinn et al. 1978) and ABA content (Guinn 1982a).

A carbohydrate deficiency may be a factor in causing the increasing rate of boll abscission with increasing boll load. Large amounts of sugars are required for boll production. Older bolls appear to be stronger sinks than young bolls; bolls seldom abscise after they pass the age of about 15 days (Guinn 1982b). Several lines of evidence indicate that a carbohydrate deficiency can increase boll abscission. (1) Complete leaf removal caused 100 percent abscission of young bolls (Mason 1922) and partial leaf removal caused increased rates of boll abscission (Eaton and Ergle 1954; Johnson and Addicott 1967) and decreased yields. (2) Low irradiance, which decreases photosynthesis (Baker 1965), stimulated boll shedding (Mason 1922; Dunlap 1945; Eaton and Rigler 1945; Saad 1951; Eaton and Ergle 1954; Goodman 1955; Brown 1971; Bhatt et al. 1972; Guinn 1974a, b, 1981; Sorour and Rassoul 1974; Vaughan and Bate 1977). (3) Boll abscission was inversely related to osmotic pressure and carbohydrate content of leaf sap (Hawkins et al. 1933). (4) Boll abscission increased when the demand for carbohydrates exceeded the supply (Hearn 1972). Factors that caused a decrease in sugar content of bolls caused an increase in their rate of eth-

ylene production (Guinn 1976a; Vaughan and Bate 1977), and the increased ethylene may have increased boll abscission (Guinn 1976a).

Depletion of N may also be a factor in causing increasing rates of boll shedding during the season. It is well known that petiole nitrate content decreases greatly during the season. Several factors probably contribute to the sharp drop in N content: (1) A cotton crop uses N during growth and fruiting; boll growth requires considerable amounts because of the protein content of seeds. (2) Nitrate leaches readily, and heavy rains or irrigation may leach some NO_3^- below the root zone. (3) Root development is inhibited by competition with bolls for carbohydrates and other nutrients (Eaton 1931; Crowther 1934; Eaton and Joham 1944). The limited growth of roots of plants with a heavy boll load limits their uptake of N.

One effect of additional N fertilizer is to extend the fruiting period and prolong the setting of bolls (Wadleigh 1944; Tucker and Tucker 1968; Hearn 1975). Jones et al. (1974) developed a computer simulation model in which N supply is a major factor regulating growth and shedding of squares and bolls. Bate and coworkers (personal communication) believe that N availability is a major factor in regulation of boll shedding.

Cultivars differ in their rates of boll shedding (Roark 1972; Verhalen et al. 1975; Patterson et al. 1978). Although different cultivars retained different percentages of their bolls, all those tested by Verhalen et al. (1975) retained a high percentage early in the season and a low percentage late in the season. In contrast, Patterson et al. (1978) found that Acala 44, a relatively indeterminate cultivar, retained a fairly low percentage of bolls early in the season and continued to retain about the same or a higher percentage later in the season. Deltapine Smooth leaf initially retained a high percentage, which decreased to low values by mid-August, but then increased again in late August and September. Partial defloration caused the percentage of bolls retained to remain high throughout the season (Patterson et al. 1978). Cotton plants with the okra leaf character produced more blooms and shed a higher percentage of their bolls than plants with normal leaves; plants with superokra leaves produced even more blooms and shed a higher percentage of their bolls than plants with okra leaves (Kerby and Buxton 1976).

Increases in boll shedding during the season are probably due to a combination of factors rather than to just one. Competition for carbohydrates, changes in hormonal status, drought, insects, and depletion of soil N may all be involved to some extent.

Square and Boll Age

Age apparently changes the sensitivity of squares and bolls to abscission stimuli. McNamara et al. (1940) followed the shedding pattern as stress developed during drought. Young bolls started shedding first, then young squares. McMichael and Guinn (1980) also found evidence that young squares were more sensitive to drought than older squares. The reason for the difference has not yet been determined.

Bolls show a remarkable decrease in shedding rate with age. This change correlates well with changes in ethylene evolution and with the capacity of the bolls to produce ethylene (Guinn, 1982b). Changes in shedding rate also correlated with changes in ABA content, but changes in ABA were not as great as those for ethylene. Ethylene evolution, ABA content, and shedding rate all decreased to very low values by 15 days after anthesis.

Changes in other hormones could also be involved. Rodgers (1977) found that IAA and gibberellin concentrations increased in bolls between about 5 and 15 days after anthesis; however, the gibberellin content was highest just after anthesis.

Structural changes could also increase resistance to shedding. Cell walls become thicker and the peduncle becomes tougher and more woody with age. Ethrel ([2-chloroethyl] phosphonic acid) caused the formation of an open abscission layer around the peduncle of mature bolls, but the peduncle did not break, apparently because the woody xylem cells were not dissolved (P. W. Morgan, personal communication).

Summary and Conclusions

In order for shedding of cotton squares or bolls to occur, cell walls in the abscission zone must be weakened by the hydrolytic enzymes pectinase and cellulase. The abscission-promoting hormones, ethylene and ABA, have been reported to stimulate synthesis of cellulase and to decrease the basipetal movement of IAA to the abscission zone. IAA normally delays or prevents abscission, possibly because it prevents the synthesis and secretion of the specific cellulase involved in abscission. Gibberellins promote abscission of explants (isolated portions of plants), but inhibit abscission when applied to cotton flowers or young bolls. Cytokinins have variable effects and may either promote or retard abscission, depending upon time and site of application. The effects of gibberellins and cytokinins may be due mainly to their ability to mobilize nutrients to the site of their application or natural distribution.

Low levels of irradiance (dim light) greatly increase boll shedding, particularly if plants have a heavy boll load. Photosynthesis is necessary to produce the organic nutrients required for boll growth. When the demand for assimilates exceeds the supply, some of the young bolls are unable to compete successfully and they shed. Hormonal changes, induced by inadequate organic nutrition, may be the signal for abscission. Starvation decreases growth rate and probably decreases the synthesis of IAA (and perhaps also cytokinins and gibberellins) and stimulates the synthesis of ethylene and ABA. These changes may cause senescence and abscission.

Cloudy weather and shading are two of the most common factors that affect irradiance at leaf surfaces. Shading, in turn, is influenced by spacing (plant population), plant height, and size and number of leaves. Plant height and leaf area are increased by adequate-to-excessive amounts of N and water and are also affected by soil type and cultivar. In areas where plants tend to grow tall (whether because of cultivar, soil type, fertility, or water supply), relatively low populations should be

used. Otherwise, a large percentage of the leaves will be shaded to such an extent that they will be unable to contribute much to total photosynthesis and some of the lower leaves may abscise because of dense shade. The portion of each plant that is in dense shade is essentially useless. Because young cotton bolls normally obtain their assimilates from nearby leaves, dense shading caused by too high a population of tall plants may cause shedding of many squares and young bolls. Older bolls seldom shed but are more subject to boll rots under these conditions. The higher the plant population, the higher the percentage of plants that are barren. Plant bug injury may also be a factor; one report indicated that the population of plant bugs increased exponentially with increasing leaf area per unit of land area. Some of these plant bugs, such as *Lygus hesperus* Knight, cause shedding of young squares.

The optimum spacing is one in which all plants are the same distance apart within and between rows. This configuration permits less crowding in the row and better light interception early in the season before plants "close the middles" in normal row spacings. Plants grown in narrow rows have been shown to fruit earlier and produce higher yields than plants grown in rows about 1 m apart. Because of operational problems, the ideal configuration of equidistant spacing is presently impractical in mechanized cotton production. The ideal plant population varies with cultivar, soil fertility, weather conditions, and irrigation. Leaf size and ultimate plant height may be used as guides; the larger the leaves and the taller the plants, the lower should be their population.

Drought increases the rate of boll shedding, apparently because it decreases photosynthesis and stimulates the rate of ABA and ethylene production in young bolls. Other hormones may also be involved. Indeterminate cultivars have been shown to tolerate seasonal drought and perform better than determinate cultivars, possibly because the indeterminate cultivars continue to direct assimilate into root growth rather than putting it all into boll growth.

Excessively high temperatures can increase boll shedding by causing pollen sterility and by increasing respiration and photorespiration. Cultivars differ in their sensitivity to heat. Selection of a heat-tolerant cultivar, irrigation to provide for evaporative cooling (transpiration) and high rates of photosynthesis, and adequate spacing to permit high rates of photosynthesis by a large percentage of leaves should alleviate the problems caused by hot weather.

Deficiencies of almost any of the essential inorganic nutrients can limit yields by slowing growth, photosynthesis, and the production of fruiting positions. Deficiencies can also increase square and boll shedding. In particular, deficiencies of N, S, Ca, B, and Zn can increase abscission. A mild deficiency of B can cause most of the fruits to abscise without limiting plant growth. Correction of micronutrient deficiencies can cause large yield increases per unit of cost; however, care should be exercised not to apply too much because toxic effects can be just as bad as, or worse than, deficiencies.

Many insects and diseases can reduce yields by decreasing plant growth, causing increased rates of square and boll

shedding, and damaging bolls that do not shed. Selection of adapted, tolerant, or immune cultivars (when available) and the adoption of cultural practices designed to provide some avoidance and control might minimize the severity of insect and disease problems without great cost.

Rates of boll shedding of determinate cultivars are typically low at the beginning of the season and increase to almost 100 percent at the time of cutout. At the same time, cotton plants almost stop growing and producing flowers. The decline in growth and fruiting and the increase in boll shedding are apparently caused by an increasing boll load, possibly because the older bolls are powerful sinks for available organic and inorganic nutrients and deprive roots, growing points, and young bolls of the nutrients needed for continued growth. When older bolls begin to mature, growth and fruiting activities are resumed if the season is sufficiently long.

Control of insects and diseases, selection of adapted cultivars, correction of nutrient deficiencies, and the use of cultural practices based on an understanding of the physiology of growth, fruiting, and abscission should maximize yields under prevailing soil and climatic conditions. The purpose of this review has been to present information that will help develop an understanding of the physiology of abscission of cotton squares and bolls. The information and concepts presented should enable the grower to differentiate between normal and abnormal shedding, and should help in diagnosing the cause(s) of abnormal shedding so that corrective action may be taken.

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Glossary

ABA.—Abscisic acid, a plant hormone that causes stomatal closure, prolongs dormancy, and may stimulate abscission.

Abscission.—An active process in plants in which an organ, usually a leaf or fruit, is lost from the plant. Same as shedding.

ACC.—1-aminocyclopropane-1-carboxylic acid, an intermediate in the synthesis of the plant hormone, ethylene.

Anther.—The part of the flower that contains pollen.

Anthesis.—The stage of development at which the fruiting form is a freshly opened flower or bloom.

Apical growth.—Growth of the apex, usually the top of the plant.

Assimilates.—Products of carbon fixation in photosynthesis.

ATP.—Adenosine triphosphate, a phosphate-containing compound that provides energy in all living organisms. ATP is one of the first products of the energy-capturing process in photosynthesis.

Auxin.—Indole-3-acetic acid. See IAA.

Boll.—A cotton fruit. The fruiting form of cotton is referred to as a boll only after it passes the flower stage.

Callose.—An insoluble polymer of glucose, a beta, 1,3-glucan, that forms in the phloem when the tissue is cut or when an abscission zone forms. Callose plugs the phloem and slows or stops leakage of sugars and other nutrients. Somewhat similar to blood clotting in animals.

Carbonic anhydrase.—An enzyme that catalyzes the reversible breakdown of carbonic acid to carbon dioxide and water.

Cellulase.—An enzyme that catalyzes the hydrolytic breakdown of cellulose to smaller molecules.

Chlorophyll.—The green pigment in plants responsible for capturing light energy for photosynthesis.

Coenzyme.—A substance necessary for the activity of an enzyme.

Coenzyme A.—A sulfur-containing coenzyme. Transfers acetyl groups in carbohydrate and lipid metabolism.

C₃ plants.—Plants in which the first product of carbon fixation in photosynthesis is a 3-carbon acid, 3-phosphoglycerate. Cotton is a C₃ plant.

Cultivar.—A cultivated variety.

Cytochromes.—Iron-containing enzymes that catalyze oxidation-reduction (electron transfer) reactions in photosynthesis and respiration.

Cytokinins.—A class of plant hormones that contain adenine and stimulate cell division.

Determinate.—A descriptive term for a reproductive habit in which a plant produces all its flowers in a short time. Strictly speaking, a determinate plant is one in which the inflorescence terminates growth as, for example, in sorghum or sunflower.

Endo-polymethylgalacturonase.—An enzyme, pectinase, that digests polymers composed of methylated galactose (pectin).

Enzymes.—Proteins that catalyze biochemical reactions in living organisms without themselves being changed.

Ethrel.—Trade name of (2-chloroethyl)phosphonic acid, a plant growth regulator that releases ethylene in plants.

Ethylene.—A plant hormone. An unsaturated 2-carbon gas, C₂H₄.

Explant.—A portion or segment of plant material surgically isolated from the rest of the plant for experimental purposes.

Ferredoxin.—An iron-containing soluble cofactor that functions as an electron acceptor and donor in photosynthesis and nitrogen fixation reactions.

Gibberellic acid, gibberellins.—A class of plant hormones that promote cell elongation and growth.

Ha.—Hectare, a unit of area equal to 2.471 acres.

Hill reaction.—One of the light reactions in photosynthesis in which illuminated chloroplasts oxidize water, release oxygen, and transfer electrons from water to a suitable electron acceptor.

IAA.—Indole-3-acetic acid, the natural auxin in plants. In cooperation with cytokinins and gibberellins, promotes cell division and growth.

IAA oxidase.—An enzyme that destroys IAA by oxidation.

Indeterminate.—A type of flowering habit in which the plant produces flowers for an indefinite time. The flowers do not terminate growth. Cotton is an indeterminate plant in the strict botanical sense, although some fast-fruiting cultivars are characterized as determinate.

Irradiance.—Incident flux of radiant energy per unit area. Light intensity.

Larva. Worm.—The wingless, wormlike, immature form of many insects.

Larvae.—Plural of larva.

Lipoic acid.—A sulfur-containing cofactor that functions in certain oxidation-reduction reactions, for example, in the reduction of sulfate. Also, a coenzyme in decarboxylation and acyl transfer reactions.

Metabolites.—Intermediates and products of metabolism in living organisms.

Methionine.—A sulfur-containing amino acid, a precursor of ethylene.

Mevalonolactone.—A chemical that can be converted to ABA in plants.

Middle lamella.—A thin layer between plant cells composed mostly of pectin.

Mitochondria.—Small organelles in plant and animal cells that contain the enzyme systems necessary for respiration and lipid metabolism.

NADPH.—The reduced form of nicotinamide adenine dinucleotide phosphate, a coenzyme that functions in photosynthesis and certain other oxidation-reduction reactions. One of the first products of the light reaction of photosynthesis. The reducing power is then used in the dark reactions of photosynthesis to produce sugars.

Nitrate reductase.—Enzyme that catalyzes the reduction of nitrate to nitrite.

Nucleic acids.—Ribonucleic acid (RNA) and deoxyribonucleic acid (DNA) are responsible for protein synthesis. DNA carries genetic information in living organisms.

Pectinase.—An enzyme that hydrolyzes pectin.

Pectin.—A cross-linked polymer of galactose sugar molecules, some of which are methylated. Occurs mainly in the middle lamella.

Peduncle.—The small stalk that supports the fruiting form (square or boll in cotton).

Petiole.—The small stalk that supports a leaf blade.

Phloem.—Specialized conductive tissue in plants through which sugars and other, mostly organic, substances move.

Photophosphorylation.—An energy-trapping process in photosynthesis in which phosphate combines with ADP to give ATP.

Photosynthate.—Organic products of photosynthesis such as sugars, starch, and amino acids.

Phospholipids.—Lipids (usually triglycerides) that contain phosphate. They occur mainly in membranes.

Polyribosome.—Structure composed of protein and messenger RNA that is the site of protein synthesis.

Pollen.—Microspores produced on the anther, the male part of the flower. Comparable to sperm in animals.

Rank.—Excessively vigorous growth, tall, leafy.

Respiration.—The metabolic process in which organic substances are oxidized to carbon dioxide and water, and the energy is conserved in the forms of ATP and NADH. (NADH is similar to NADPH, but functions in respiration rather than in photosynthesis.)

Senescence.—An aging process in which a plant part loses its chlorophyll (turns from green to greenish yellow), enzyme activities, and the ability to retain metabolites and grow.

Sinks.—Plant parts to which nutrients flow. Rapidly growing bolls are strong sinks.

Stigma.—The part of a flower that serves as the site for pollen germination.

Stomatal closure.—A process for conserving water in which stomates close to restrict passage of gasses into or out of plant tissue.

Stomates.—An area comprised of paired kidney-shaped cells (guard cells) on the surfaces of leaves and, to a lesser extent, other plant parts, and a hollow area beneath known as the stomatal cavity.

Square.—The triangular-shaped flower bud of cotton. The fruiting form is called a square before the flowering stage and a boll after flowering.

Thiamine pyrophosphate.—A sulfur- and phosphate-containing cofactor that functions in the decarboxylation of certain organic acids.

T9.—A designation for a particular strain of *Verticillium albo-atrum* (a fungal disease organism that causes verticillium wilt) that causes rapid defoliation (loss of leaves by abscission).

Translocation.—A process by which substances are moved from one part of a plant to another.

Tryptophan(e).—An amino acid that is a precursor for IAA synthesis.

Xylem.—Conductive tissue in plants that connects roots to other plant parts. Contents are water, inorganic nutrients, and certain organic substances such as amino acids and cytokinins.