

Chapter 14

PHYSIOLOGY OF DEFOLIATION IN COTTON PRODUCTION

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INTRODUCTION

The cotton plant is inherently a deciduous perennial with a natural mechanism for shedding its mature leaves. During the growing season the leaves function to supply photosynthates to the developing fruit and shed only when the leaf or plant undergoes a stress such as drought, disease, starvation or frost. Once the entire crop is mature, however, the leaves serve no useful purpose, and their removal can be beneficial for mechanical harvesting. Reducing the large amounts of foliage in preparation for harvest has become an important step in the production of high-quality fiber.

Chemical defoliation is a cultural practice which induces abscission of cotton foliage earlier than normal (National Cotton Council, 1949). The practice received its greatest impetus with the advent of mechanical harvesters during the 1940's and is now considered one of the major beltwide practices. Defoliant chemicals are applied to half or more of the cotton grown annually in the United States to facilitate mechanical harvest. For spindle picking, the complete removal of all leaves without killing any of the remaining plant becomes the desirable condition. The machine itself may operate with high efficiency if only a small percentage of leaves remain, but succulent green leaves may stain the lint, and dead dry leaves will fracture to become "pepper" trash in the ginned lint (National Cotton Council, 1950).

Cotton leaf abscission is a physiological process that involves an active separation of living tissue from the plant. An understanding of the basic aspects of the process is essential to successful defoliation of cotton with exogenous chemicals. This topic is the subject of a number of recent articles and reviews (Addicott, 1970; Addicott and Wiatr, 1977; Carns, 1966; Guinn, 1979; Rubinstein and Leopold, 1964; Walhood and Addicott, 1968).

THE NATURE OF DEFOLIATION

Leaf abscission in cotton is usually a result of maturity, senescence or injury. The maturity or senescence state of development, however, is not always related to age in days or months but is more often a reflection of the conditions under which the plant develops. Leaves can become senescent and shed from the plant through the influence of a number of stress situations. Such stresses, however, may be considered as injuries or unfavorable alterations of vital plant processes. The application of chemicals for defoliation merely involves the use of an applied injury that ultimately induces the plant to abscise its leaves. Abscission, whether due to natural or induced senescence, is usually preceded by a variety of senescent changes. These include: a loss of chlorophyll; increased anthocyanin; reduced levels of proteins, carbohydrates and inorganic ions (Walhood and Addicott, 1968; Addicott, 1969); and alterations in hormone concentrations (Addicott and Lynch, 1955; Carns, 1966; Burg, 1968; Addicott, 1969; Del la Fuente and Leopold, 1968).

The cotton leaf petiole has an area near its base that is structurally distinguishable and characterized by a structural line of weakness where abscission occurs (Figure 1). Toward the end of the senescence process, there is a dramatic increase in metabolic activity within this abscission zone. The increased activity results from alterations of the hormone levels of the leaf blade which in turn alter the hormone levels within the abscission zone (Rubinstein and Leopold, 1964; Abcles, 1967; Leopold, 1971; Webster, 1973; Osborne, 1974; Addicott and Wiatr, 1977). Thus, abscission is controlled by an interaction of hormones. These hormonal interactions cause cells within the abscission zone to secrete hydrolytic enzymes that degrade the cell wall, especially the pectic substances of the middle lamella and cell walls, to permit the leaf to fall from the plant. Although a number of enzymes are recognized as increasing in activity within the abscission zone in correlation with abscission (Addicott and Wiatr, 1977), pectinase and cellulase have been investigated most extensively (Durbin *et al.*, 1981; Horton and Osborne, 1967; Lewis and Varner, 1970; Morr , 1968; Reid *et al.*, 1974; Riov, 1974). These enzymes are synthesized in the plasmalemma and secreted into the middle lamella region where they digest the middle lamella and hydrolyze portions of the primary cell wall (Sexton and Hall, 1974). The weakened cell walls eventually permit separation, and the leaf falls from the plant. Abscission may not occur immediately, however, because the vascular tissue is not affected by the enzyme activity but must be broken by mechanical forces. These forces are supplied by the weight of the leaf blade plus a shear and tension action created by cell division and enlargement on the stem side of the abscission zone and cell shrinkage on the leaf side (Morr , 1968; Leopold, 1971; Osborne, 1973). The cell division on the stem side also produces a corky protective layer across the leaf scar (Walhood and Addicott, 1968). The differential cell growth across the abscission

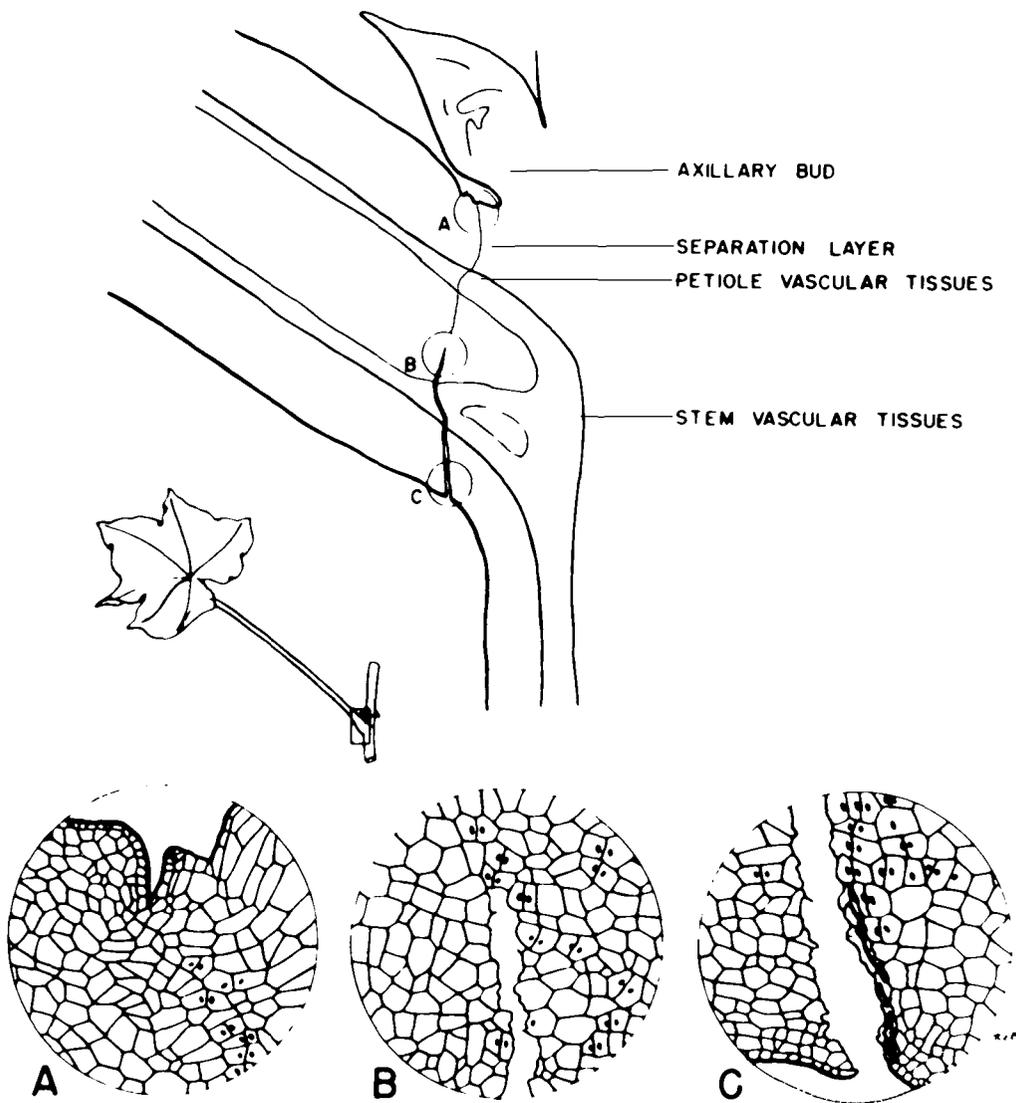


Figure 1. Diagram of the leaf base of cotton during process of defoliation. Circles A-C correspond with the drawings which show relationship of cell divisions to separation layer. Separation occurs between dividing cells on the distal side of the abscission zone. Cell divisions, followed by separation, commence at the lower edge of the abscission zone and progress upward. (By Katharine C. Baker)

zone may explain observations reported by McMichael *et al.* (1973) and Osborne (1974). They reported that leaves failed to abscise during periods of water deficit, but that abscission occurred readily after the deficit was relieved by watering. Both of these observations lend support to the suggestion of Addicott and Lynch (1955) that actual leaf separation is a growth process that requires turgor.

Although leaf abscission results from enzymatic dissolution of cells in the abscission zone, the process is influenced by hormone levels within the leaf blade and external environmental factors. Defoliant chemicals are used to alter the hormonal balance and induce abscission; however, the efficacy of most defoliant chemicals may be influenced by environmental factors as well as the hormone levels within the plant.

HORMONAL EFFECTS

The major hormones that are known to have one or more important influences on abscission include indole and naphthalene acetic acid (IAA and NAA), abscisic acid (ABA), gibberellic acid (GA), ethylene (ETH) and cytokinin (CK) (Addicott and Wiatr, 1977). In addition, the literature contains evidence that several other endogenous substances such as amino acids, senescence factors (SF) and ascorbic acid may affect abscission (Addicott, 1970; See also chapters 12 and 13). Generally the auxins (IAA and NAA) retard abscission while the plant hormones, ABA and ETH, are promotive. The influences of GA and CK are variable depending on interactions with several other factors. The exact mechanism by which plant hormones regulate abscission is not fully understood; however, several theories have been advanced. These are discussed in detail in the reviews by Carns (1966) and Rubinstein and Leopold (1964).

The auxin-gradient theory of abscission control proposed by Addicott *et al.* (1955) states that relative concentrations of auxin on each side of the abscission zone are more important than the absolute auxin concentration. The theory is based on observations that IAA inhibits abscission when applied to the petiole side of the zone, and stimulates abscission when applied to the stem side (Addicott and Lynch, 1955; Addicott *et al.*, 1955). They proposed that abscission is initiated only after a shift in auxin gradient across the abscission zone is favorable to the stem side. They also suggested that decreased auxin production by leaf blades during the process of growth and maturation caused a gradual auxin gradient shift to occur and initiate abscission in senescent leaves. This may help to explain the observed increased responsiveness of mature leaves to defoliant chemicals.

More recently Rubinstein and Leopold (1963) proposed the "two-stage" theory of abscission control by auxin. They suggested that abscission response to auxin can be divided into an inhibitory stage followed by one of promotion. The theory was based on observations that time of auxin application to petiole stumps was just as important as concentration. They found that the abscission effect of auxin shifted from inhibition to promotion as the time between deblading and

application increased. Similar results were obtained from stem applications. While the theory was based on results obtained with NAA, similar results were obtained with IAA (Chatterjee and Leopold, 1963).

The function of ABA in abscission is primarily promotive, and as suggested by Addicott and Wiatr (1977), may be associated with all abscission. The effect may be indirect, however, since it has been shown to stimulate ETH production (Cracker and Abeles, 1969; Jackson and Osborne, 1972), hasten senescence (Del la Fuente and Leopold, 1968), and decrease auxin transport (Chang and Jacobs, 1973). Direct effects of ABA have also been reported. Cracker and Abeles (1969) found that ABA increased the cellulase enzyme activity in the abscission zone of both cotton and bean (*Phaseolus vulgaris*) explants.

Ethylene has long been known as a potent abscission-promoting hormone. Its effect is similar to that of ABA in that the effect can be either direct or indirect. Direct effects include stimulated synthesis of pectinase (Riov, 1974) and cellulase (Horton and Osborne, 1967; Abeles, 1969; Ratner *et al.*, 1969; Reid *et al.*, 1974) in the abscission zone. In addition, ethylene causes increased secretion of enzymes into cell walls to enhance cell wall digestion (Abeles *et al.*, 1971).

Addicott and Wiatr (1977) suggested that the promotion of abscission by ETH may come more from its influence on the levels of other hormones than from direct effects. Morgan and Hall (1962) showed that ETH increased decarboxylation of IAA and stimulated the activity of the IAA-oxidase system. These events suggest a mechanism for reducing auxin concentrations in the leaf tissue and would tend to promote abscission. In addition, ETH has been shown to decrease or inhibit auxin transport (Morgan and Gausman, 1966; Beyer and Morgan, 1969, 1971) which in itself tends to promote abscission (Morgan and Durham, 1975). Thus, the combined effect of IAA degradation in the leaf tissue and the auxin transport inhibition through the petiole decreases the amount of auxin that reaches the abscission zone, and abscission is promoted.

The auxin-ethylene interaction has also been used to explain the auxin-gradient and "two-stage" theories of abscission control. Auxin stimulates ETH production in plant tissue (Morgan and Hall, 1962), and according to Abeles (1967), when applied to the stem side of the abscission zone, the ETH moves more rapidly than the auxin to the separation layer and promotes abscission. But, when auxin is applied to the petiole side, the auxin moves faster than the ETH, and abscission is inhibited. Leopold (1971) explains that during stage I of the "two-stage" theory the tissue is relatively insensitive to ETH, and auxin inhibits abscission. However, during stage II the tissue becomes sensitive to ETH, and the auxin inhibiting effect is overridden by the abscission-promoting effect of ethylene.

The effects of gibberellins on abscission are considered as moderately promotive, although conflicting reports are contained in the literature. The effect imposed by GA apparently depends to a large extent on application site and interactions with several other factors. Brian *et al.* (1959) sprayed the foliage of deciduous woody plants with GA and observed delayed senescence, renewed shoot

growth, and retarded abscission. Walhood (1958) obtained similar results when cotton foliage was sprayed with GA. Addicott and Wiatr (1977) reported that GA had a promotive effect when applied to the abscission zone and an inhibitory effect when applied to the leaf. The GA tended to promote vigor in the treated leaf and indirectly inhibited abscission. In more sensitive tests where explants were used as test material, GA was found to accelerate abscission when applied to either side of the abscission zone (Carns *et al.*, 1961). Chatterjee and Leopold (1963) obtained similar results with a wide range of concentrations of GA. They concluded that GA served to accelerate stage I of the "two-stage" response theory. GA has also been shown to enhance ETH activity (Morgan and Durham, 1975).

Cytokinin has a moderate retarding effect on abscission when applied to either the abscission zone or leaf blade (Addicott and Wiatr, 1977). Rogers (1981b) made comparative analyses of retained and naturally abscising cotton plant organs and found that abscission was negatively correlated with CK concentration. Apparently the effect of CK is indirect and is caused by prevention or delay of senescence in plant organs; delayed senescence reduces the sensitivity to the abscission-promoting effects of ETH (Del la Fuente and Leopold, 1968; Leopold, 1971). Evidently the delayed senescence and retarded abscission are related to increased ability of the organs to compete for metabolites (Letham, 1967). Cothren and Cotterman (1980) reported significant decreases in transpiration and nitrogen loss from CK-treated leaves. They suggested that the CK altered metabolism in favor of delayed senescence.

In addition to the well-established plant hormones that regulate abscission, there is beginning to be some evidence of one or more special senescence-promoting hormones. (Noodén and Leopold, 1977). The chemical nature of the material is still somewhat obscure, so it is referred to as "senescence factor" (SF). Osborne *et al.* (1972) postulated that it functions as a regulator of ETH production, thereby tending to initiate abscission. It is considered of general occurrence in plants but is separated from the site of ETH biosynthesis by membrane compartmentation and released only after injury or senescence.

Since amino acids in high amounts are found in leaves and petioles prior to abscission (Leinweber and Hall, 1959b), they may be important regulators of natural leaf abscission. A number of amino acids were found to promote abscission when applied to explants and de-bladed petioles; these include alanine, glutamic acid, serine, glycine, aspartic acid, phenylalanine, methionine, glutamine and histidine (Rubinstein and Leopold, 1962). Most of these have been reported to function during stage II of the "two-stage" response theory (Rubinstein and Leopold, 1963). Abscission enhancement apparently results from increased senescence (Martin and Thimann, 1972), enhanced ETH production (Rubinstein and Leopold, 1964) and increased hydrolytic enzyme synthesis (Addicott, 1969, 1970).

It becomes apparent from reviews of reports in the literature that the mechanism of leaf abscission involves the complex actions and interactions of many

substances that control the activity of the pectinase and cellulase enzymes within the abscission zone. The plant hormones most directly involved include IAA, NAA, ABA, and ETH. Other substances, however, may have indirect effects through their effects on synthesis and transport of these hormones and other plant metabolites.

EXOGENOUS CHEMICAL DEFOLIATION

After the accidental discovery of exogenous chemical defoliation of cotton in the late 1930's, research indicated that it was feasible to remove leaves from a cotton crop before it was harvested (National Cotton Council, 1949). Since then, numerous chemicals have been screened in search of efficient defoliant materials. Most, however, have been discarded because of cost, poor field performance, or other disadvantages. Results from much of this work have been reported at the annual Beltwide Cotton Defoliation and Physiology Conferences (now named Beltwide Cotton Physiology Conference) (National Cotton Council, 1947-82). The search continues and a few promising chemicals are being tested at present under experimental label.

Formulations of magnesium and sodium chlorate were among the earliest products used extensively as cotton defoliants, and both are still in widespread use across the Cotton Belt. They are relatively inexpensive products and are very effective, especially when leaves are fully matured; they have little effect on immature leaves or on regrowth vegetation. Both chemicals are equally effective when applied at equivalent active ingredient rates. The two organophosphorus compounds (S,S,S-tributyl phosphorotrithioate, DEF; and S,S,S-tributyl phosphorotrithioate, merphos, Folex) are highly efficient defoliants and frequently cause leaf fall before excessive drying occurs. They often will remove immature leaves and are relatively effective in removing regrowth vegetation. Cacodylic acid (hydroxydimethylarsine oxide) is formulated as sodium cacodylate and is used extensively as a cotton defoliant in the western United States where leaves are consistently tougher than those further east. Limited testing of the product in Mississippi indicates a tendency towards excessive desiccation of leaves in the terminal portion of the plant (Cathey, 1979).

Two of the more recently developed defoliant chemicals are Harvade® (dimethipim) (2,3-dehydro-5,6-dimethyl-1,4-dithiin-1,1,4,4-tetraoxide) and Dropp® (thidiazuron) (N-phenyl-N'-1,2,3-thiadiazol-5-ylurea). The two chemicals are about equal in their effect on cotton leaf abscission, and the effect is comparable with that caused by either the chlorates or the phosphates (Ames, 1981; Taylor, 1981). Both chemicals, however, are superior to either the chlorates or the phosphates in the inhibition of regrowth (Hopkins and Moore, 1980).

The effect of defoliant chemicals on cotton leaves is similar to that of leaf blade removal, *i.e.*, the hormone balance is altered so that the auxin supply to the abscission zone is insufficient to inhibit initiation of the abscission process (Carns,

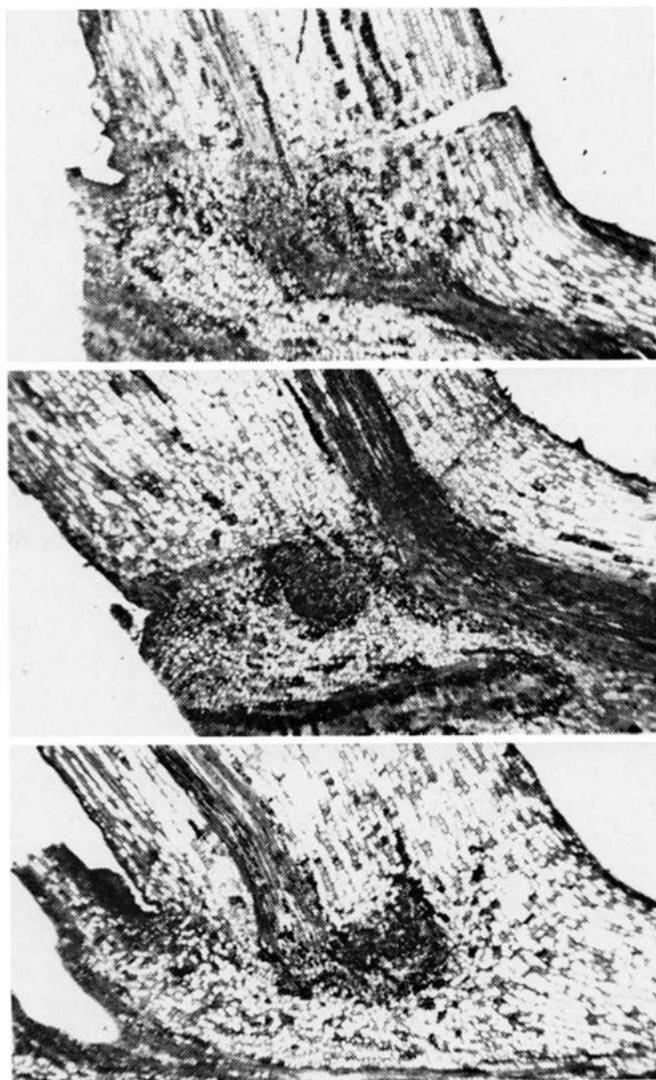


Figure 2. Photomicrographs of abscission zone of cotton illustrating abscission response to a defoliant chemical. At the bottom is shown a cross section of the abscission region before defoliant application. The center photo shows growth of the separation layer after application, while in the top picture, the leaf petiole begins to separate from the stem. (Photos by Vernon L. Hall)

1966). It appears unlikely, however, that chemically-induced defoliation results from any specific physiological action by the defoliant chemical, since there is such variance in their chemical structure and in the injury produced. Not all chemicals that injure cotton leaves are capable of stimulating abscission, and even with the most effective defoliants the degree of injury must be properly regulated (cf. Walhood and Addicott, 1968). Excessive injury may kill the tissue in the abscission zone and prevent the vital processes required for abscission. Conversely, low levels of injury may fail to initiate the process. The degree of injury induced by most defoliant chemicals varies with plant condition, defoliant concentration and environmental factors. Defoliant chemical injury is usually visible on the leaf blade within 48 to 72 hours of application, and the separation layer in the abscission zone becomes visible 1 or 2 days later (Figure 2). Under normal field conditions the defoliation process is complete in 7 to 14 days, but in some situations may be delayed for as long as 30 days.

The condition of the plant and the prevailing weather at time of application are the major factors that limit efficiency of the defoliation process. In general, efficiency is highest when plants have become vegetatively dormant and reproductively mature; when moisture content of the leaf is high; and when both temperature and humidity are high (National Cotton Council, 1950). Before abscission can take place, the leaf must be in a condition of activity that will allow the proper degree of reaction to the defoliant. There also must be sufficient activity to allow for the biological processes that initiate the abscission process. An ample moisture supply helps to ensure adequate leaf physiological activity. Under conditions of prolonged drought the leaves frequently become toughened and are reduced in physiological activity. The cells in the blade and petiole of such leaves fail to react properly to the defoliant chemical and defoliation is inadequate (McMichael *et al.*, 1973; Osborne, 1974).

While an ample supply of both moisture and nutrients is desired throughout the growing season for uniform growth and development, the supply of each should be almost exhausted at defoliation time. Defoliation is especially enhanced when the nitrogen supply is low or depleted (Addicott and Lynch, 1955). In addition, excessive supplies of these elements late in the season tend to promote renewed vegetative development that responds poorly to defoliant chemicals. The newly developed leaves have not developed the state of senescence required for rapid abscission. Defoliation efficiency has been found to be directly related to age of leaves when plants have been in a continuous state of growth (Brown and Rhyne, 1954). Usually the lower leaves and the leaves subtending mature bolls are more responsive to most defoliant chemicals than are the leaves of the newer growth (Addicott, 1968; Thomas, 1965).

Weather conditions at the time of application or for 3-5 days afterwards can have an important influence on plant response to defoliant chemicals. Defoliants are most active when temperature, sunlight intensity, and relative humidity are high. A night temperature above 16C is particularly important. Under controlled

conditions Lane *et al.* (1954) found that plant response to a defoliant doubled for each 10 degree rise between 15C and 35C. They reported that only 40 percent of the leaves had fallen from plants after 21 days in a constant 15C temperature regime. When the diurnal temperature average was 24C, the abscission rate was rapid and a high percentage of the leaves fell.

A high relative humidity is also best for defoliant action, because it contributes to leaf surface conditions that allow optimum reaction to the chemical (National Cotton Council, 1950). With high relative humidity, evaporation and transpiration are reduced, the internal moisture of the leaf remains relatively high, and the chemical is retained in a liquid state on the leaf surface for a longer period of time. These conditions promote absorption of the chemical into the leaf, which is necessary to begin the physiological process of abscission.

The response to defoliant chemicals is reduced during periods of cloudy weather. The nature of the reduced effect is not fully understood, although, usually lower temperatures are associated with cloudy weather. Brown and Hyer (1954), however, reported that extended dark periods reduced the effectiveness of defoliants on plants grown under controlled conditions. This suggests that more factors than temperature are involved.

Although the use of chemicals to prepare cotton for harvest has been commercially successful for over 40 years, there are still many failures. Most of the failures are related to either plant or environmental conditions that are not conducive to maximum plant response to the defoliant chemical. In efforts to increase plant response to defoliants under these adverse conditions, numerous components have been used as additives to the defoliant mixture. These additives include various surfactant-type chemicals as well as products that have senescent and/or abscission-inducing properties. The effectiveness of many of these additives has not been well established, however.

Brown (1957) reported that surfactants increased the effectiveness of defoliant chemicals in Arizona, but results in Mississippi have been inconsistent, even when used in adverse environments (Cathey, 1979). The addition of an endothall [7-oxabicyclo-(2.2.1)heptane-2,3-dicarboxylic acid] formulation usually causes slightly earlier leaf drop, but by the seventh day after application results are similar to those from the defoliant treatment alone (Ford *et al.*, 1970; Cornelius *et al.*, 1970). There is a possibility, however, of a synergistic effect when endothall is used in combination with defoliants (Davis *et al.*, 1972; Sterrett *et al.*, 1973). The addition of small quantities of paraquat (1,1'-dimethyl-4,4'-bipyridinium ion) to defoliant chemicals, applied after adverse weather conditions develop, has increased abscission of juvenile leaves in plant terminals (Kirby and Stelzer, 1968; Cornelius *et al.*, 1970). Morgan and Durham (1975) used gibberellic acid to enhance ethylene-induced abscission and suggested that GA might improve the performance of several of the defoliant chemicals.

The experimental growth regulator chemical TD-1123 (potassium 3,4-dichloro-isothiazole-5-carboxylate) was used successfully to induce senescence in

cotton leaves and caused an increased response to subsequent defoliant treatments (Arle, 1976; Cathey, 1978). Defoliation was increased by as much as 25 percent, without an adverse effect on yield or quality, when TD-1123 was applied 10 days before the regular defoliant treatment. Sequential treatments of TD-1123 and the defoliant have an apparent synergistic effect on several physiological events that occur during the abscission process (Elmore *et al.*, 1978; Cathey *et al.*, 1981c). For example, most parameters that are affected by a defoliant chemical are not altered by TD-1123 but become more pronounced and occur earlier in sequentially treated leaves. Relatively low rates of defoliant chemicals have been used to accomplish effects similar to those caused by TD-1123 (Thomas, 1965; Cathey and Hacskeylo, 1971). This is not a widespread practice, however, because of inconsistent results and an occasional excess of premature leaf fall (Thomas, 1965). Sequential treatments with defoliant chemicals apparently increased defoliation by affecting both states of the "two-stage" abscission process. Cathey and Hacskeylo (1971) reported consistent improvements in defoliation when a given quantity of a defoliant chemical was applied in sequential applications rather than as a single treatment.

SUMMARY

Cotton leaf abscission is a physiological process that involves an active separation of living tissue from the plant. As leaves become senescent because of age, stress or injury, the process is initiated and leaf fall follows. Separation occurs in a specialized area of the leaf petiole located near its base and is characterized by a line of weakness across the petiole. The mechanism of leaf abscission involves complex actions and interactions of many substances within the plant as well as various external factors. The abscission process is the result of increased pectinase and cellulase activity within the abscission zone that degrades the walls and middle lamella of cells of the separation layer. This enzyme activity, however, is regulated by the hormone balance within the plant. The major hormones involved include IAA, ABA, ethylene, GA and cytokinin. The auxins IAA and NAA are strong inhibitors of abscission while ABA and ethylene are primarily promotive; gibberellic acid and cytokinin have variable effects depending upon concentration, site of application and tissue involved.

Exogenous chemical defoliation is a cultural practice used to induce abscission of cotton foliage earlier than normal. It has become an important practice in the production of high quality fiber and is considered a necessary aid to machine harvesting when yields are high and plants have green succulent foliage. Defoliant chemicals are used to induce sufficient leaf injury that will alter the hormone balance of the plant and initiate the abscission process. Several products are commercially available that have this ability; however, their effectiveness varies with plant and environmental conditions that prevail at application time. Maximum efficiency with most defoliants require that the plants be uniformly devel-

oped and have a large percentage of the leaves relatively mature and free of moisture stress. In addition, atmospheric temperature and humidity should be relatively high. A few products have been developed for use as additives to defoliant chemicals to enhance defoliation under adverse plant and environmental conditions. Their effectiveness is questionable, however, and none of these products are in widespread use.