Chapter 4

INFLUENCE OF ATMOSPHERIC PARAMETERS ON GROWTH AND DEVELOPMENT

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INTRODUCTION

The genus, *Gossypium,* evolved in tropical, drier parts of the world. In spite of man's efforts to alter the species from a nominally Mediterranean climate-adapted, photoperiodic perennial to a temperate annual, it still bears the attributes of its tropical origins in that it is somewhat drouth tolerant and prefers warm temperatures and sunshine. Alteration of the major climatic variables of temperature, water, light, photoperiod, and mineral nutrition can drastically alter initiation and retention of fruit forms and plant senescence.

FLOWER INITIATION

The initiation of fruiting branches is influenced primarily by day length and temperature. The number of fruiting branches can be influenced by plant spacing or defruiting. Many of the tropical stocks of the geographic race *latifolium* are photoperiodic (Tomar, 1965; Mauney and Phillips, 1963); however, commercial American upland cottons which were derived from *latifolium* are essentially insensitive to day length. Many of the wild *latifolium* strains do show response to temperature and water balance in addition to day length (Hutchinson, 1959). In their natural habitat, the wild cottons normally produce leaves, flower, and set fruit following the wet summer season, and then defoliate and mature the fruit during the dry winter season.

Mauney and Phillips (1963) studied floral initiation in 36 lines representing 24 species. Day neutral and both short and long day photoperiodic types were noted. Commercial upland varieties initiated flowering with little or no evidence of photoperiodic response. However, they recorded as much as three nodes delay in fruiting branch initiation in both *G. hirsutum* and *G. barbadense* on 14-hour days as compared to 10-hour days. Low *et al.* (1969) also investigated the effects of day length, radiation, and temperature levels on commercial varieties of *G. hirsutum* and *G. barbadense.* Their results parallel those of Mauney (1966). High temperatures raised node number of the first fruiting branch, particularly those of late or indeterminate *G. barbadense* lines. Longer day length delayed fruiting in both species but more so in *G. barbadense.* Low temperature promoted earliness in fruiting, but there was considerable influence by genotype.

A greater effect on flower initiation is shown by high temperature. Earlier reports (Dastur, 1948) indicate that lower night temperature favors vegetative branching. More recent studies by Mauney (1966) indicate the reverse; i.e., that high night temperatures (25C) delay flowering in upland regardless of day temperature. A day temperature of 25C combined with a lower (20C) night level enhanced flowering. *G. barbadense* (Pima) was also delayed in flowering by high day-night levels but the day temperatures exerted greater control.

A number of researchers at Texas A&M University (Kohel and Richmond, 1962; Kohel *et al.,* 1965; Kohel and Lewis, 1970; Lewis and Richmond, 1957; Waddle *et al.,* 1961; Kohel *et al.,* 1974) studied the inheritance of flowering response to environment in *G. hirsutum* and *G. barbadense.* In *G. barbadense* flowering is controlled by only a few genes with photocontrol dominant to day neutral. In photoperiodic *G. hirsutum,* flowering is controlled by the cumulative effect of multiple genes. Delays in flowering were noted in crosses between *G. hirsutum* day neutral and *G. hirsutum* non-flowering (presumably photocontrolled) (Kohel *et al.,* 1974).

The plant growth stage, when temperature treatment is applied, has some influence. Germination temperature can alter flowering branch initiation one node. The temperature after seedling emergence (7 days of germination) is of major importance in differentiation of the first fruiting branch. Thus, lower night temperatures during the immediate post emergence period can be instrumental in lowering the node of first fruiting. Chilling temperatures during germination can markedly delay time to first flower (Christiansen and Thomas, 1969) but does not alter the node level of first flowering branch. The chilling effect is on overall plant growth and development.

Recent greenhouse experiments show little or no effect of ambient air polluting oxidants on the initiation of flowering in eight commercial varieties of cotton, including seven uplands and one *G. barbadense* variety (Heggestad and Christiansen, 1978). Apparently, there has been little work directed at the role of light intensity or quality in relation to fruiting induction. Nor has there been any definitive research with increased CO_2 to enhance flower induction. One might conjecture that improvement of reserve metabolites in developing plants might speed the induction of flowering.

THE NATURE OF FLOWER AND FRUIT ABSCISSION

Two major theories have been developed to explain the incidence and variation in fruit set in cotton. The hormone theory, as set forth by Addicott and Lynch (1955), involves a balance of auxin and growth retarding or anti-auxin hormones on proximal and distal sides of a potential abscission site. As boll load increases, production of anti-auxins increase and set of new fruit forms is reduced. An alternate theory holds that the organic nutritional status of the plant determines the quantity of fruit set. As an increasing number of bolls is added to a plant, the supply of carbohydrate lessens and new fruit forms are dropped (Chapter 12). A part of the evidence to support either the nutritional or hormone theory of fruit retention control lies in an examination of the response of photosynthesis, respiration, and plant hormone status to light, temperature, and gaseous environment.

PHOTOSYNTHESIS AND RESPIRATION RESPONSE TO ENVIRONMENT

A treatise concerned with the effect of varying light quantity and quality, temperature and CO_2, O_2, and air pollutants on fruit retention should be concerned with the relationship of photosynthesis and plant nutritional status. Each of these environmental parameters directly influence photosynthesis and respiration and, therefore, may be controlling factors in establishing carbohydrate status of the plant.

Temperature—Temperature dependency of photosynthesis follows a normal curve with an optimal range and minima at each end of the temperature range. Cotton is moderately tolerant to heat. Photosynthesis is depressed 40 percent after 15 minutes at 46C (Esipova, 1959) as compared to a 95 percent depression of *Phaseolus vulgaris* in 5 minutes (Lyutova, 1952). No data are available for minimum temperature suppression but one would conjecture that 12-15C would be restrictive. Respiration is drastically reduced at 8C in cotton leaves (Amin, 1969). Most chilling sensitive species, including cotton (Amin, 1969; Stewart and Guinn, 1971) display greatly reduced respiration at temperatures below 10-12C (Lyons and Raison, 1970). Net photosynthesis (P_n) for cotton shows a broad temperature optimum ranging from 25-45C with a total extinction point near 55C (El-Sharkawy and Hesketh, 1964). These data were collected from greenhouse plants cultured at relatively high temperatures. The responses were obtained from turgid, light saturated, detached leaves. The authors suggest that under such experimental conditions, P_n optima tend to be higher than when whole plants are used.

CO_2 and O_2—Throughton (1975) reported environmental effects on CO_2 uptake in cotton. Temperature exerted little effect or was not limiting to the initial photosynthetic rate at 100 ppm CO_2 or less. At higher CO_2 levels, uptake was restricted by temperatures of 12-18C. At 23, 26, and 33C, CO_2 level increased the photosynthetic rate at a linear rate to 300 ppm CO_2. Oxygen exerted an inhibitory effect on CO_2 uptake; e.g., uptake photosynthesis maximized in the absence of O_2 at 150 ppm CO_2. If oxygen was 22 percent, CO_2 fixation maximized at 300 ppm; at 44 percent O_2 the maximum CO_2 uptake at 400 ppm CO_2 was approximately 60 percent of the zero oxygen level (Chapter 17).

Air Pollutants—Oxidants in general suppress photosynthesis in higher plants as does fluoride and SO_2 if the pollutant levels are sufficiently high to induce chlorosis. Ozone, the most common air pollutant, has perhaps the most immediate effect on gaseous exchange in plants. When leaves are exposed to ozone, the stomate guard cells quickly lose turgidity, stomates close, and gas exchange is greatly reduced (Bennett, 1969). There is little direct information on cotton published, but there is ample evidence with many species to show that sub-lethal dosages of ozone markedly reduce photosynthetic activity. Although cotton is listed among the crops resistant to ozone (Hill *et al.*, 1961), recent studies by Heggestad and Christiansen (1978) indicate considerable genetic variation in sensitivity. Sensitive varieties respond with reduced fruit set, lower yields, and earlier cut out. Studies by Dugger *et al.*, (1966) on many species including cotton have demonstrated that ozone exposure causes a significant reduction in total carbohydrate, but an increase in reducing sugars and respiration, the latter perhaps as a consequence of readily metabolizable hexose sugar. Bennett (1969) reported an inhibition of starch synthesis by ozone. Possibly ozone inhibition of photosynthesis coupled with stimulated respiration causes tissue starvation, premature senescence, leaf abscission and early cut-out. Controlled studies with ozone while keeping temperature, humidity, water, and mineral conditions at optimum could perhaps serve to elucidate the nutrition-hormone relations of fruit drop. Unfortunately, ozone stress likewise induces ethylene, and thus the nutritional and hormone situation is again unseparable.

LIGHT, TEMPERATURE, OR GASEOUS STRESS EFFECT ON HORMONE STATUS

A considerable volume of information has developed in the past decade concerning stress induction of abscisic acid (ABA) and ethylene in plants. A number of papers relate water stress (Allaway and Mansfield, 1970; Little and Eidt, 1968; Wright and Hiron, 1964) and osmotic stress (Mizrah *et al.*, 1970) with increases in ABA. Ethylene induction also is related to a wide array of injuries and stresses including insect injury (Williamson, 1950), warm nights (Guinn, 1976), low temperatures (Vines *et al.*, 1968), drouth (McMichael *et al.*, 1977; Jordan *et al.*, 1972), virus infection (Ross and Williamson, 1951), fungus disease (Wiese and

DeVay, 1970), mechanical injury (Abeles, 1973) and low light (Guinn, 1976). A secondary effect of ABA induction may well be increases in ethylene (Abeles, 1967).

BASIC EFFECTS OF ENVIRONMENT ON ABSCISSION

Normal, healthy, well-nutured leaves or fruit forms do not abscise. Injury, disease or senescence normally predates development of abscission. Variation in environmental factors to the point of stressing the plant can contribute to induction of the "abnormal" condition conducive to abscission. A number of aerial environmental factors including temperature, light, CO_2, O_2, and pollutants are known to affect abscission in controlled and field conditions.

In general, response to temperature by the abscission process is similar to other vital plant responses. Low temperature reduces the rate of action and a higher temperature stimulates activity (Yamaguchi, 1954). Extreme temperatures in the nature of chilling, freezing, or heat stress incite abscission as an injury response. Extreme temperature stresses which kill plant tissue usually prevent abscission because the abscission process is dependent upon viable tissue. A short photoperiod is generally correlated with induction of abscission (Garner and Allard, 1923). Autumn leaf fall is, thus, thought to be triggered by day length in certain species (Olmstead, 1951).

The gaseous environment can alter abscission under controlled conditions. For example, increased oxygen levels stimulate abscission of bean explants (Carns *et al.*, 1951) over a range of 0 to 50 percent; and increases of CO_2 tend to retard abscission in explants. The ability of ethylene, a natural air contaminant, to induce abscission is well documented (Abeles, 1967). Present evidence indicates that ethylene operates to decrease auxin in the petiole (Morgan and Durham, 1975) and increase enzymes that are involved in the activation of the abscission zone. Considerable information indicates that abscisic acid (ABA) induces ethylene which in turn induces abscission (Craker and Abeles, 1969; Abeles *et al.*, 1971). We (unpublished data) noted an inhibitory effect of rhizobotoxin (an inhibitor of ethylene synthesis) on ABA induction of abscission in cotton explants. This strongly suggests that environmental stress can exert an effect through induction of ABA, which induces ethylene, which in turn triggers abscission. Other non-hormone air pollutants such as ozone, SO_2 or NO_x are noted for ability to hasten senescence of leaves.

EFFECTS OF ENVIRONMENT ON FRUITING

Much of the early research to elucidate the factors contributing to fruit abscission pointed to plant nutrition or to the theories that "the cotton plant only retains bolls that it can feed." The early work of King and Loomis (1932) and Hawkins (1933) supported the nutritional idea as did that of Wadleigh (1944). In many studies, low carbohydrate status was correlated with abscission. For example, application of sucrose retarded or reduced abscission in certain species (Went and Carter, 1948; Brown and Addicott, 1950), and girdling of plant stems to prevent downward translocation of sugars, so they would accumulate above the girdle, reduced abscission in fruit (Chandler, 1925).

In contrast to the above supportive evidence, Eaton and Ergle (1953) noted little difference in the mid-August carbohydrate status of early (high shedding rate) and late plantings (low shedding rate). They presented contradictory data from sugar applications and girdling studies to refute the involvement of nutritional status in boll shed.

Gibson and Joham (1968) found that low night temperature favored increased flowering and fruit set but reduced boll development. In complimentary research at the same location, sugar levels in developing bolls were monitored (Krieg *et al.*, 1968). Maximum sugar concentration (7 mg/g tissue) was found in 10-day old bolls at 25C night temperature. At lower temperatures (10-15C and 20C), sugars maximized after 15 days at about 60 percent of the level of the 25C treatment but remained at 4-5 mg/g tissue for up to 30 days boll age, while the 25C treatment dropped to 2 mg/g tissue or less. The simple sugars predominated in early boll development and sucrose gradually increased to predominate at 30-35 days of boll age. The dominate sugar during early boll development was fructose. The idea that high night respiration will deplete simple sugars and induce abscission is not supported by the data of Krieg *et al.*, (1968) in that fructose was highest at 25C and lower at 10-15-20C.

In recent years, Guinn (1974a, 1976a, 1977) has presented definitive data to support the nutritional thesis and to relate nutritional status with increases in ABA and ethylene and thus with theories regarding hormonal (especially ethylene) control of fruit abscission. Using low light and temperature manipulation to alter carbohydrate status, Guinn correlated ethylene evolution with carbohydrate status and related both to fruit set in cotton. He concluded that "the nutritional and hormonal theories of shedding are not mutually exclusive because a nutritional stress may increase ethylene evolution enough to promote abscission."

In a greenhouse comparison of filtered and non-filtered air, Heggestad and Christiansen (1978) reported prolonged growth, delayed senescence, and greater boll set on plants cultured in filtered air. Genetic differences in pollution tolerance were shown with Acala varieties being most tolerant and Paymaster 202 most sensitive. Brewer and Ferry (1974) reported a two-year study in California on the field assessment of pollution effects. They noted yield increases from 10 to 30 percent by cotton grown in filtered air in plastic enclosed field plots as compared to cotton grown in non-filtered air in comparable enclosures. Senescence was delayed several weeks by filtered air and boll set was increased at two locations (Parlier and Hanford) in the San Joaquin Valley. Much of the increased yield was attributed to prolongation of the flower-set period and delay of senescence. Ting and Dugger (1968) related ozone sensitivity in cotton to leaf age, finding that immature leaves were most susceptible to damage, and that older leaves were insensitive to ozone. Taylor and Mersereau (1963) induced marked symptoms of early senescence and early leaf fall with controlled ozone treatments.

High temperature and high relative humidity are cited as major factors in reduced fruit retention in cotton. Meyer (1969) reported an increase in sterile anthers at temperatures above 38C with a time lag of about 15 days between exposure to heat and expression of sterility. Sarvella (1966) noted adverse effects of wind, high evaporation conditions, and high solar radiation on pollen viability. Stress occurring two to three weeks prior to anthesis induced the sterility. Fisher (1973) has negatively correlated minimum temperature with boll set in Arizona. Humidities in extremes of 21 and 90 percent reduced boll retention while 40-65 percent was favorable (Hoffman and Rawlens, 1970). Ehlig and LeMert (1973) conducted extensive field studies attempting to correlate ambient temperatures and humidities with fruit retention under various defruiting treatments. They noted little effect of high temperature on boll retention *per se.* Although they do not preclude the possibility that high temperature or high or low humidity affect boll retention, their field data indicate that boll load is the major contributor to fruit drop. They observed brief periods of unusually high (48-49C) temperature that affected fruit set, but they suggest that such conditions are not common. They also noted that brief periods of low solar radiation adversely affected boll retention. (See Chapter 20)

ENVIRONMENTAL STRESS AND "CUT OUT"

Mason (1922) regarded the slowing of late season growth and the ultimate cessation of terminal activity (cut out) as due mainly to the diversion of carbohydrates to developing bolls. Heath (1932) observed that plant development to first flower was relatively constant; after first flower the growth rate declined. Crowther (1934a) related cessation of growth to a diversion of plant nitrogen (N) from the growing points to accompany carbohydrate transfer to developing bolls. He noted a drop in root N uptake to zero and ascribed reduced root development to reduced carbohydrate supply to the roots.

General observations by many researchers relate most environmental stresses with retardation of growth in cotton and to induction of senescence of leaves and inactivation of terminals. The presence of bolls, as indicated by defruiting studies, has an accelerating effect dependent upon the quantity present on the plant.

Excessively high or low temperature, reduced light, noxious air pollutants (ozone) or a restriction of water or nutrients will greatly hasten "cut out." Relief of boll load and amelioration of the stress usually stimulate a resurgence of growth. This sort of habit is perhaps retained from cotton's Mediterranean climate ancestors in which vegetative growth, flowering, fruiting, and seasonal quiescence were regulated by the wet season—dry season habitat. Breeders have managed to isolate genetic lines less affected by environment and thus indeterminate in growth and fruiting. Very determinate types also have been developed that respond by "cut out" to boll load and environmental stress. The ultimate effect of fruit retention is to suppress terminal bud activity.

SUMMARY

The presently available literature supports the following: Extremes of the aerial environment including high or low temperature, low light, short days, long nights (especially at warm temperatures), air pollutants including ozone, SO_2, NOx, or ethylene can alter initiation of flowering, reduce retention of fruit, and hasten the time to senescence of the cotton plant. The impact of environmental stress is accentuated if plants are well fruited.

Each of the above adversities also have been related to reduction or alteration of carbohydrate levels in the plant, with induction of ABA and/or ethylene by stress or injury which can be related to fruit drop. The recent definitive data of Guinn (1976a) provides the most pursuasive argument that the nutritional and hormone theories can be blended into a single description of the sequence of events controlling fruiting and senescence.

Although ethylene increases and abscission may be induced with little alteration of carbohydrate status, there appears to be a continuation of events from stress → ABA → ethylene → abscission that includes a drop in carbohydrate. Whether alteration of carbohydrate is a salient circumstance brought on by stress closure of stomates or a driving force is not clearly elucidated by present data, although the large volume of data on low light effect on carbohydrate decreases and abscission increase is supportive.

The present information framework has certain deficiencies but when the entire structure is complete, I think that it will include both nutritional and hormonal control mechanisms.