Chapter 7

WATER DEFICITS AND REPRODUCTION

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INTRODUCTION

Soil water availability is one of the primary edaphic factors which act to influence, and perhaps even control, production of potential fruiting points, retention of squares and bolls and yield of cotton. The role of soil water availability is both direct, in the sense that it may influence the internal plant water balance, and indirect, in that it may alter mineral nutrient availability, soil-borne pathogen and insect activities, and soil temperature. In this Chapter only the direct effects of soil water availability on plant water deficit, and the attendant effects on production, retention, and growth of fruiting forms are considered, but it must be pointed out that seldom are the indirect interactions observed or quantified. More comprehensive discussions of water relations and water management are found in recent reviews by Hearn (1979) and Jordan (1983).

CONTROL OF FRUITING PROCESSES

The production of fruiting forms is discussed in detail by Mauney in Chapter 2 and will not be repeated herein except to emphasize certain important points. The first point is that production of potential fruiting forms is dependent upon vegetative growth. Actual numbers of potential fruiting forms depend upon the rate of production of successive nodes and upon the ratio and location of vegetative and fruiting branches. Reductions in vegetative growth rates associated with low soil water availability are often reported; therefore, production of total fruiting forms must also be reduced.

A second point relates to the balance between vegetative and reproductive growth. Numerous reports relating square and boll shed to periods of drought or irrigation cycles suggest that the retention of immature reproductive structures is extremely dynamic and responsive to brief perturbations in water supply. These environmental disturbances are manifest in the growing plant as either alterations of the current nutritonal status of the plant and/or as disruptions in the hormonal balance such that the flow of hormones necessary for normal maintenance of the abscission zone is interrupted. Neither explanation alone fully

accounts for the accelerated loss of young squares and bolls in crops subjected to prolonged or periodic water deficit. It is likely that the history of soil water availability throughout the growth of the crop may influence the operative mechanism in square and boll shed.

The discussion above regarding the role of available soil water in control of vegetative growth provides a convenient introduction to the topic of control of fruiting and yield in the contrasting situations of dryland versus irrigated production. Plant water deficits arising from the inability of the crop to extract soil water in sufficient quantities to match transpiration are commonly reported to occur in both production systems. However, significant differences in the timing, duration, magnitude and rates of development of plant water deficits do occur between the two systems and bear heavily on yield-related processes. Much of the following discussion is speculative, since little documented evidence exists upon which to base a critical evaluation of the role of water deficits directly on the fruiting process.

SOIL WATER AVAILABILITY AND VEGETATIVE GROWTH.

Dryland production areas are characterized by extreme variations in the total water supply available to the growing crop. Since large variations occur both within and among seasons, seldom do repeatable patterns of soil water deficit occur. In these situations, many years of field data are required to establish even crude relationships between soil water supply and yield. The effect of increasing amounts of available soil water at planting time on yield are amply illustrated in the reports of Fisher and Burnett (1953) and Bilbro (1974) for the Rolling and High Plains of Texas, respectively, but these reports shed little light on the reasons for reduced yield, i.e. reduced potential fruiting points, loss of fruiting forms or reduced boll sizes. Since low yields under dryland conditions often reflect a small total above ground biomass, an examination of the relation of vegetative growth to soil and plant water status may provide a means to evaluate the primary causes of low yields. Several reports bear on this topic.

In an early report by Hancock (1941), evidence was presented that yield was closely associated with the rate of increase in plant height during the period of maximum growth rate. Later reports by Bruce and Shipp (1962), Bruce and Romkens (1965), and Rijks (1965) substantiated this height-yield association and provided additional information which illustrated that production of total fruiting points and fruits was quantitatively related to plant height (Figure 1). A single curve (Figure 1a) adequately described the square production per plant for two levels of soil water management (mean matric potentials of -0.3 bars and -0.6 bars in the 15-45 cm soil zone for treatments A and B, respectively), illustrating that the production of total fruiting points (squares) exhibited the same or greater sensitivity to soil water deficit as vegetative growth. The total fruit load also
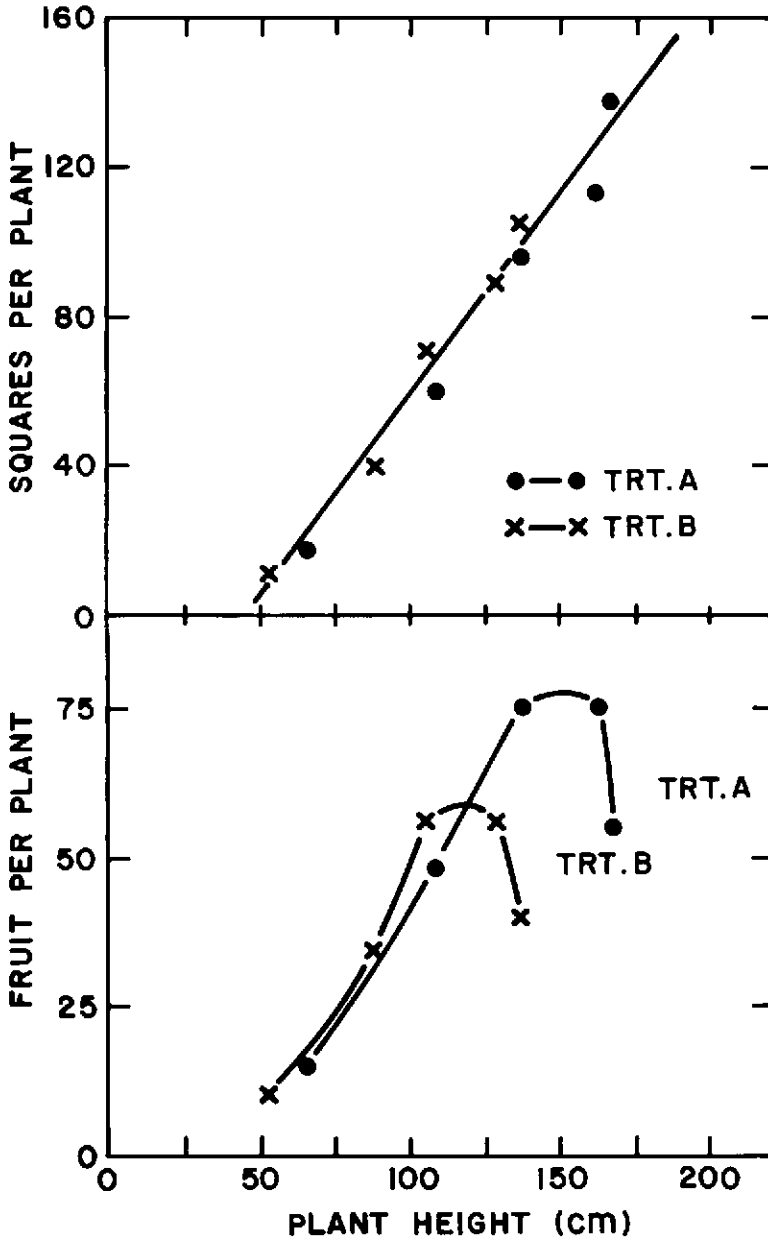
Figure 1. The relation between plant height and (upper) square production, and (lower) fruiting as influenced by two levels of soil moisture. Moisture levels A and B, corresponding to soil matric potentials of -0.03 to -0.06 MPa in the 15-45 cm soil zone, were maintained throughout the study. (Data from Bruce and Romkens, 1965).
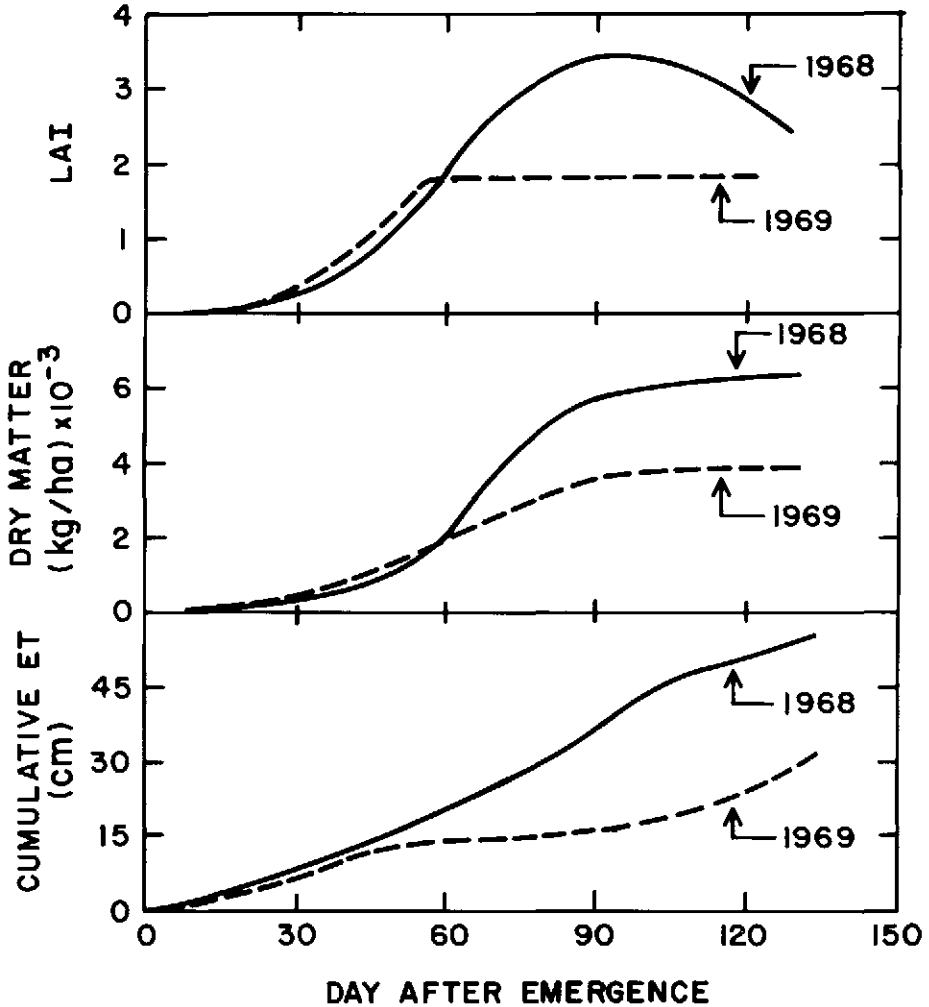
Figure 2. Changes in (top) leaf area index (LAI), (middle) total above ground dry
    matter, and (bottom) cumulative evapotranspiration (ET) with time after
    planting for cotton crops produced under rain-fed conditions at Temple, TX in
    1968 and 1969. (Redrawn from Ritchie and Burnett, 1971).

exhibited a nearlinear relation to plant height during early fruiting (Figure 1b),
but a peak in fruit load was reached about four weeks after first bloom regardless
of soil water level. The total fruit load was reduced by the lower soil water
treatment (TRT B).

Vegetative growth, water use and dry matter accumulation for upland cotton

(Lankart 57) grown under rain-fed conditions at Temple, Texas are shown in Figure 2 (Ritchie and Burnett, 1971). These results may be considered typical for many regions which depend upon stored soil water plus substantial summer rainfall to achieve satisfactory yields. Total crop growth was greatly reduced in 1969 relative to 1968 because of a prolonged period without rain in June and July. By 60 days after emergence (DAE), increases in leaf area for the 1969 crop had stopped and further increases in dry matter were probably associated with boll growth (i.e., 'cutout'). The harvest index (lint wt./total above ground dry wt.) for 1968 and 1969 was 0.078 and 0.073, respectively. Under conditions where plant water deficits developed gradually, the partitioning of dry matter between above-ground vegetative matter and lint remained relatively stable. Similar results were also reported by Eaton (1955). Bolls which developed from early flowers comprised 100 percent of the yield in 1969; late season rainfall was ineffective because of the cessation of active vegetative growth and late season insect pressures.

The importance of early boll retention to yield under water-limited conditions is illustrated clearly by the data of Rijks (1965) for plants grown on stored soil water (Table 1). Plants grown with low water supply (140 mm) produced fewer nodes, fewer fruiting branches and fewer fruiting forms, but retained a high

Table 1. Growth and boll load characteristics of cotton plants grown with increasing amounts of available soil water. Based on data from Rijks (1965). Data are expressed on a per plant basis except for lint yield.

Character	Available soil water (mm)			
	140	340	460	670
Total nodes	21	28	38	39
Total fruiting branches	6	10	19	24
Bolls				
Total	6	18	35	50
At 1st fruiting position	5	9	13	21
Squares shed	2	7	42	58
Boll retention (%)	75	72	45	46
Boll position ratio (%)[1]	83	50	37	42
Lint yield (kg ha^{-1})	160	439	732	1030

[1]The ratio of bolls at the first fruiting position on fruiting branches to total bolls.

percentage of squares (75 percent). Since growth of fruiting branches was also restricted by water deficit, a high percentage of bolls were located at the first fruiting position, illustrating the importance of high fruit set from early flowers for water-limited situations. Failure to control insect pests early in the season results in additional yield reductions and lower water use efficiency in terms of lint per unit water used. Reported water use efficiencies for rainfed crops range between 0 and 0.45 kg lint per m^3 water, but most values fall in the range of 0.1 to 0.3 kg/m^3 (Hearn, 1979).

Several additional insights were gained through an intensive study of the water balance of the 1969 crop. Data presented in Figure 2 provided evidence that, even though vegetative growth (leaf area) had ceased by 60 days after emergence (DAE), transpiration and total dry matter continued to increase for several weeks. This finding suggests a differential sensitivity existed between the plant water deficit required to inhibit growth and that required to cause stomatal closure (Hsiao, 1973; Jordan, 1970; Wadleigh and Gauch, 1948). A similar conclusion was reached by Hearn (1979). A detailed diurnal study conducted on July 17-18 (82 DAE) revealed that stomates of upper leaves remained open throughout the day even though leaf water potentials were reduced to -27 bars (Jordan and Ritchie, 1971). Since, for greenhouse and chamber grown plants, the threshold leaf water potential for stomatal closure commonly occurs about -15 bars (personal observations and Jordan and Ritchie, 1971), we concluded that the long period of exposure to plant water deficit allowed the field plants to become acclimated to successively lower potentials. This finding was subsequently confirmed and extended (Brown *et al.*, 1976; Cutter and Rains, 1977; Thomas *et al.*, 1976) and is now generally accepted as one manifestation of osmoregulation that occurs in many crop species in response to drought (Begg and Turner, 1976). Recent work by Radin and coworkers (1981, 1982) suggests N-nutrition may also play an important role in regulating plant response to water deficit (See Chapter 10).

WATER DEFICIT-INDUCED ABSCISSION

Characteristics of plant water deficit patterns which develop in irrigated cotton are usually quite different from those experienced by a rain-fed crop. Plant water deficits associated with irrigation cycles are usually developed rapidly, relatively short in duration, and frequently severe enough to result in wilting for several days. Numerous studies during the past 50 years have addressed the question of optimum timing for application of supplemental water. No attempt will be made to summarize these reports; however, several common results are pertinent to this topic and will be discussed below. The stated or implied objective of most of these studies was to optimize the efficient use of applied water in terms of yield of marketable lint and seed.

As a point of departure into this topic, it is desirable to restate an earlier observation, i.e. within limits, the production of potential fruiting points must be closely allied with vegetative growth. Because of high soil water availability, the rate and maximum extent of canopy development in the irrigated crop is usually much greater than for rain-fed areas. Maximum leaf area indices (LAI) for rain-fed cotton are often near 3 and may range from 1 to 4, while for a fully irrigated crop values over 5 are common (Ashley *et al.*, 1965; Ritchie and Burnett, 1971). Rapid canopy development is also associated with higher rates of soil water use since the crop will use water at rates equal to the potential evapotranspiration

after an effective full canopy (LAI = 3) is reached and so long as water remains fully available to the roots (Ritchie and Burnett, 1971). Since the water holding capacity of many soils in areas under full-season irrigation is quite low, and extraction rates are high, plant water deficits may develop over a period of only a few days in contrast to several weeks in rain-fed areas. Wilting is commonly observed near the end of irrigation cycles and, in fact, is used to time water applications in some areas.

The detailed studies of Grimes *et al.* (1969, 1970) and Stockton *et al.* (1961) serve to illustrate the influence of irrigation frequency on plant growth, flowering and boll retention in situations considered typical for irrigated cotton production. Grimes *et al.* (1970) reported that a severe plant water deficit imposed during the peak flowering period reduced yield more than a comparable deficit occurring either earlier or later in the flowering period. Water deficits early in the flowering period increased shedding of squares before they flowered, while late stress reduced flowering rate and boll retention.

These results were similar to a more extensive earlier study by Stockton *et al.* (1961) covering a period of four years. Intermediate irrigation frequencies resulted in production of fewer flowers, but the numbers of bolls retained was equal to treatments receiving twice as many irrigations. Only on infrequently irrigated plots was vegetative growth reduced. The concomitant reduction in flower production resulted in fewer bolls per plant even though a higher percentage of bolls were retained (see also Table 1 and Hancock, 1941). The pattern of boll set in relation to irrigation frequency was variable. No discernable pattern was found for the most frequently irrigated treatment; however, a definite tendency for increased boll retention was associated with the day of irrigation in the two less frequently watered treatments. For the most infrequently watered treatment nearly three times as many bolls were set on the day of irrigation as on the day midway between water applications.

The cyclic nature of boll set for infrequently irrigated plots is suggestive of a shedding mechanism controlled not only by plant water deficit, but also by the number of bolls set per day. In this study (Stockton *et al.,* 1961) both stimuli were evident. Midway between irrigations plant water deficits predominated as the causative agent in boll abscission. Immediately following water additions there were periods of high boll set followed by a period of high boll shed before water deficit recurred.

The study discussed above provides a possible basis upon which to evaluate the nutritional and hormonal hypotheses of fruit shed outlined in the review by Eaton (1955) and more recently summarized by Guinn (1982b and Chapter 12). In the absence of other external limitations, the balance of growth between vegetative and reproductive structures is closely regulated by the carbohydrate and nitrogen status of the plant. The balance is achieved by overproduction of fruiting forms which are then shed in numbers necessary to match the carrying capacity of the plant at a specific time. The dynamic nature of this form of control is illustrated

by the rapid increase in fruit shed associated with cloudy weather or artificial shading (Eaton, 1955; Guinn, 1974a, 1976a). Stockton et al. (1961) speculate that the resumption of shedding after irrigation cannot be explained on the basis of nutrition since even a high retention of young bolls (1-3 days old) would not constitute a substantial sink for photosynthate. However, the resumption of active leaf expansion following irrigation may constitute an additional sink of major importance. Also, the interpretation by Stockton et al. (1961) regarding demand by bolls set on the day of irrigation may be questioned. While it is true that sink strength of 1-3 day old bolls is not great, these bolls would have been several days older midway between irrigations and may have constituted an appreciable demand for photosynthate. The total demand for carbohydrate and nitrogen to support renewed vegetative growth as well as additional numbers of young bolls may be sufficient to trigger shedding, especially if photosynthetic rates do not recover as quickly as turgor. Fry (1972) reported that Hill reaction activity of chloroplasts isolated from stressed leaves showed a steady decline of about 1.8 percent per bar as leaf water potential decreased from -0.9 to -3.0 MPa. Ackerson et al. (1977) observed that rates of net photosynthesis declined dramatically during drought even though stomatal conductance decreased only slightly. Reduced chloroplast activity and net photosynthetic rates may both be related to the loss of chloroplast integrity and increased hydrolytic activity associated with dehydration, as discussed by Vieira da Silva (1976). The rate of recovery of chloroplast integrity or net photosynthetic rates is not known for cotton, but results from other crops suggest turgor and transpiration recover more quickly.

The possibility that plant water deficits may directly act to induce shedding must also be considered. Assuming the sequence of events is the same in fruit abscission as in leaf abscission, plant water deficits may act to trigger several changes in the balance and rate of supply of phytohormones to the abscission zone. Briefly stated, the hormonal theory of abscission deals with the rate of supply of juvenile (principally auxin) and aging or senescence hormones from the leaf blade or fruit to the abscission zone (Beyer and Morgan, 1971; Carns, 1966; Eaton, 1955; Guinn, 1982b). The separation layer in this zone is maintained in a normal 'healthy' state so long as the juvenile hormone activity predominates, but should the balance shift in favor of the aging or senescence hormones, then irreversible changes are triggered in these cells which result in eventual separation.

Changes in concentrations of several phytohormones are associated with development of plant water deficits of a magnitude known to induce leaf and boll abscission (Guinn, 1976b; McMichael et al., 1972b). Ethylene production increases (Guinn 1976b; Jordan et al., 1972; McMichael et al., 1972a) as does the concentration of abscisic acid (ABA) (Davenport et al., 1977a; Jordan et al., 1975). Ethylene appears to play multiple roles in abscission including reduction in auxin transport to the abscission zone (Beyer and Morgan, 1971), induction of hydrolytic enzyme synthesis and secretion of these enzymes into walls of cells in

the separation layer (Abeles, 1969; Abeles *et al.*, 1971). It is unclear at this time if all actions are manifest by plant water deficit-induced ethylene production. Recent evidence suggests a strong association between plant water deficit and reduced auxin transport (Davenport *et al.*, 1977b), but whether this effect is independent of ethylene action is not known. Transport of other growth regulators (ABA, kinetin, gibberellic acid) does not appear to be affected by plant water deficit (Davenport *et al.*, 1977a; 1979) in young seedlings.

SUMMARY

In summary, the roles of plant water deficit in regulation of production and retention of reproductive structures of cotton appear to be manifest in two general ways. Plant water deficits induced by low available soil water and/or high evaporative demand reduce the total number of potential fruiting points as a result of a general reduction in shoot growth. Provided these deficits are developed gradually over a long period of time, a stable balance between vegetative and reproductive growth is maintained. Deficits imposed early in the growth of the crop and maintained throughout much of the fruiting period may result in early cutout, if the plant water deficit falls below that needed to support positive cellular turgor necessary for growth. Photosynthesis may continue for a time even though growth is inhibited because the stomatal apparatus may acclimate through osmoregulation. Thus, dry matter accumulation and boll growth may continue even though vegetative growth has stopped. Stress-induced cutout may therefore be a qualitatively different process from normal cutout resulting from high nutritional demand by developing fruit (Eaton, 1955; See also Chapter 2).

Plant water deficits that occur rapidly near the end of irrigation cycles appear to exert effects on fruiting and flowering apart from a general reduction in growth. Rapid development of deficits may limit the capacity of the plant to acclimate and results in an alteration of the normal hormone balance of the abscission zone. In this regard, deficit-induced stimulation of ethylene production and reduced auxin transport appear to be most important, but rates of production of auxin and abscisic acid may also be altered. Once induced, abscission requires active growth of cells near the separation layer which may explain differences in abscission patterns between field and pot studies. Cellular growth requires turgor which is normally reestablished each night in field-grown but not in pot-grown plants (Jordan and Ritchie, 1971; McMichael *et al.* 1972a,b). If abscission-inducing levels of water deficit are encountered during the day, nighttime rehydration allows necessary growth, and abscission occurs during the drying cycle. Since overnight recovery does not normally occur in severely stressed plants grown in pots with limited soil volumes, abscission is often not observed until the pots are rewatered. Shedding then occurs rapidly during the next few days.

While an explanation of abscission in response to rapid water stress may be based on changes in the normal hormone balance, a nutritional explanation may

also be offered. A cessation of vegetative growth would likely accompany any water stress sufficient to induce shedding. While cell expansion may be inhibited, cell division may continue, thereby creating a sink for growth substrates when rehydration occurs. This vegetative sink may be sufficient to reduce substrates available for boll growth and shedding of young fruit may result. Even though possible, a few problems may exist with this explanation. Cell division and cell expansion may have different thresholds and sensitivities to plant water deficit, but since severe deficits may occur rapidly for irrigated plants, it is questionable whether a great deal of cell division would occur after expansion is inhibited. Also, since photosynthesis may continue at deficits where expansion is reduced, a higher supply of carbohydrate would be available in leaves to support resumed growth, thereby minimizing the effect on young fruit. These conflicts remain to be resolved.