Chapter 10

THE NITROGEN STRESS SYNDROME

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INTRODUCTION

This paper will present and discuss some basic physiological effects of nitrogen (N) nutrition in the cotton plant. The general thesis will be that N deficiency generates several related, yet discrete and experimentally identifiable, effects. Overall, these effects are integrated at the whole-plant level to produce systematic alterations in growth, yield, earliness, and other agronomic characteristics.

Because the benefits or detriments of a particular level of N nutrition are conditional—dependent upon other factors—the concept of N deficiency must be defined closely here. By deficiency we mean a level of N nutrition which allows less than maximum dry matter production without regard to the nature of that dry matter. Thus, to the extent that N nutrition alters partitioning between vegetative and reproductive dry matter, a deficiency could actually be desirable. Indeed, this argument is made for cotton grown under certain conditions and probably is valid for indeterminate crops in general.

There are three primary responses by plants to N deficiency which can explain most or all of their observed differences in growth and performance. These three effects are: (1) altered photosynthetic rate; (2) altered leaf expansion resulting from changes in hydraulic conductivity; and (3) altered responses to water stress. The first effect has received by far the most attention, presumably because chlorophyll depletion is the most obvious visual symptom of N deficiency. All three effects, however, contribute to alterations of whole-plant behavior. In fact, except for severe deficiency, the second and third effects may be the most important. Each of the three effects is discussed in a separate section of this paper, and an integrative overview is presented in the final two sections.

PHOTOSYNTHESIS

The literature is replete with studies of the relationship between plant N status and photosynthetic rate. There is little need to review this literature extensively. Ojima *et al.* (1967) present a typically strong correlation between leaf photosyn-

thetic rate and leaf N concentration. Natr (1975) examined this subject and concluded that photosynthetic rate per unit leaf area was closely related to leaf N concentration.

There is little reason to doubt an effect of N on photosynthesis, although Radin (1983a) argued that photosynthetic inhibition is secondary to other effects of N deficiency as a determinant of growth in cotton (and other dicotyledonous plants). In cereals, growth effects of N deficiency were much more closely tied to photosynthesis (Radin, 1983a). Because most of the leaf N is in the chloroplasts (Stocking and Ongun, 1962) and most of the chloroplast N is in the enzyme RuBP carboxylase (Kleinkopf *et al.*, 1970), various authors have concluded that N regulates photosynthesis through its gross effects on the extractable activity of this enzyme (Natr, 1975; Medina, 1970). The evidence for this conclusion remains weak because it remains strictly correlative (*e.g.*, Motta and Medina, 1978). The critical data (*e.g.*, increased concentrations of RuBP, the substrate, and decreased concentrations of PGA, the reaction product) under N deficiency have not yet been published.

Photosynthesis can be considered to consist of "dark reactions" and "light reactions" (see Chapter 15). The former (which include the CO_2 fixation step catalyzed by RuBP carboxylase) are generally believed to limit photosynthetic rate in high light, but not in dim light. Some work suggests that N deficiency inhibits photosynthesis in low light to about the same extent as in high light (Nevins and Loomis, 1970; Osman and Milthorpe, 1971; Natr, 1970; Andreeva *et al.*, 1971 cited in Natr, 1975). Thus, it seems unlikely that carboxylation would be the only step influenced by N deficiency. Again, these observations are not supported by critical work to identify the presumed limiting step in the light reactions. Although chlorophyll levels are obviously affected by N, there is no reason to conclude that they become insufficient for normal photosynthesis (Benedict *et al.*, 1972).

Another possible interpretation of these data is that N deficiency might alter the activation level of RuBP carboxylase. This enzyme is activated by binding CO_2 and Mg (Jensen and Bahr, 1977). Recent evidence suggests that low light limits photosynthesis by regulating the degree of activation of RuBP carboxylase; its activity remains rate-limiting despite the low light (Perchorowicz *et al.*, 1981). The possible relationship between N nutrition and RuBP carboxylase activation remains unexplored.

Medina (1971) showed that N deficiency in *Atriplex patula* caused large accumulations of starch which were correlated with loss of photosynthetic activity. He suggested a possible causal role of the starch in photosynthetic inhibition. Deleterious effects on photosynthesis under some conditions have frequently been attributed to starch (cf. reviews by Neales and Incoll, 1968; Guinn and Mauney, 1980). Nafziger and Koller (1976) attributed starch effects to an increased diffusion pathlength for CO_2 within the chloroplast, but there is no direct evidence for this or any other mechanism. A possible role of starch in N-deficient

plants has not been followed up. It is worth pointing out that this proposed effect of N is fundamentally different from the others discussed earlier—inhibition by starch, an end product of photosynthesis, implies that photosynthetic changes occur fairly late in the progression of N deficiency. Obviously, other effects of N must first cause the accumulation of starch before photosynthetic effects could be seen.

Effects of N on photosynthesis at the chloroplast level are evidenced by changes in the mesophyll resistance to CO_2 diffusion. The well-known model of Gaastra (1959) envisions sequential resistances in the pathway for CO_2 uptake, *i.e.* stomatal and mesophyll resistances in series. Recently, Wong *et al.* (1979) reported that these two resistances were closely related under a variety of conditions, including N deficiency. Thus, in analyzing limitations to photosynthesis, one must consider effects on the entire diffusion pathway. The spectacular advances in plant biochemistry of the last 20 to 30 years have tended to focus attention on the chloroplast, but studies of photosynthesis involving the stomata have not kept pace. Nonetheless, some work has appeared which implicates them in the effects of N deficiency. Childers and Cowart (1935) early showed that N deficiency sharply curtailed transpiration rate along with photosynthetic rate of apple leaves. Ryle and Hesketh (1969), Nevins and Loomis (1970), and Ludlow and Ng (1976) much later demonstrated increased stomatal resistance due to N deficiency in corn, sugarbeet and *Panicum maximum*, respectively. The changes paralleled those of the mesophyll resistance to CO_2 uptake. Further convincing evidence for N effects on stomata was provided by Ishihara *et al.* (1978, 1979a,b) in rice. Although their use of stomatal aperture measurements instead of stomatal resistances largely precluded any precise partitioning of N effects into stomatal and mesophyll components, it is clear that stomatal closure caused a substantial part of the N-related changes in photosynthesis. However, Medina (1970, 1971) found no evidence for a stomatal component of the N effects in *Atriplex patula*.

Are the N effects on stomatal and mesophyll resistances independent or coupled, and if coupled, what is the mechanism? Teleologically it makes sense for stomata to close partially when the mesophyll resistance increases, for this would minimize the expenditure of water per unit of photosynthesis (Wong *et al.*, 1977; Cowan and Farquhar, 1977). The most commonly proposed coupling mechanism involves CO_2. Stomata often are found to close as intercellular CO_2 concentration increases (Meidner and Mansfield, 1968; Sheriff, 1979). Farquhar *et al.* (1978) proposed that photosynthesis (which depletes the intercellular pool of gaseous CO_2) and stomatal resistance (which controls the rate of replenishment of that pool) interact to stabilize the intercellular CO_2 concentration. This hypothesis has found wide acceptance, although it is not universally applicable because stomata are not always CO_2-sensitive (Zelitch, 1969).

Raschke and coworkers (Raschke, 1975; Raschke *et al.*, 1976; Dubbe *et al.*, 1978) demonstrated that in several species, stomatal sensitivity to CO_2 depends

upon abscisic acid (ABA). Radin and Ackerson (1981) confirmed this in cotton. Neither N-deficient nor normal plants showed stomatal sensitivity to CO_2 unless the leaves had been sprayed with ABA or unless the plants were subjected to water stress. The effects of water stress on stomatal sensitivity to CO_2 persisted for at least a day after rewatering (Radin, unpublished). Presumably water-stressed plants were responding to endogenous ABA, which accumulated as a result of the water stress (Radin and Ackerson, 1981). However, the situation is complicated by the discovery that in N-deficient cotton, stomata began to show CO_2 sensitivity very early in the stress cycle and long before the leaf wilted or displayed any other visual symptoms of water stress (Radin and Ackerson, 1981). Thus, N-deficient plants, which are apparently well-watered, might or might not be entering a water stress-induced phase of stomatal CO_2 sensitivity. Based upon these results, it is impossible to judge whether the N effects on stomata discussed earlier all resulted simply from CO_2 homeostasis. The acceptance of this hypothesis for N-deficient leaves should be accompanied by specific tests of CO_2 sensitivity.

Other types of possible N effects on stomata, such as changes in elasticity of guard cell walls, have not been proposed or investigated. Presumably any such structural effects would be possible only if N were deficient during leaf (and guard cell) development. In experiments of Ryle and Hesketh (1969) and Nevins and Loomis (1970), N was withdrawn after leaves were mature, and such a mechanism presumably could not account for the results. However, it should be noted that N deficiency during leaf enlargement greatly decreased the elasticity of mesophyll cell walls (Radin and Parker, 1979a).

LEAF EXPANSION AND HYDRAULIC CONDUCTIVITY

It has long been known that N nutrition affects the partitioning of plant resources into tops and roots. Turner (1922) found large differences in top:root ratio due to N availability, and he cited several similar findings from the middle of the 19th century. The recognition that this resulted from a more or less specific effect of N on leaf area is often credited to Watson (1952), who used growth analysis to separate leaf area development from dry matter accumulation. However, the same phenomenon was clearly shown earlier by others, for example Crowther (1934). Similar differences between N effects on leaf area growth and photosynthesis or dry matter increases have since been shown by Bouma (1970) and De Jong and Phillips (1981). Responses of cotton to N are typical (Figure 1). In plants grown on nutrient solutions in an artificial environment, dry matter accumulation per unit leaf area (net assimilation rate) was much less sensitive to N availability than was leaf area increase per unit leaf area (relative leaf area growth rate). These changes correspond to dry matter partitioning into leaves of about 65 percent at the highest N level and 45 percent at the lowest N level. Obviously this is a very substantial difference in photosynthate translocation

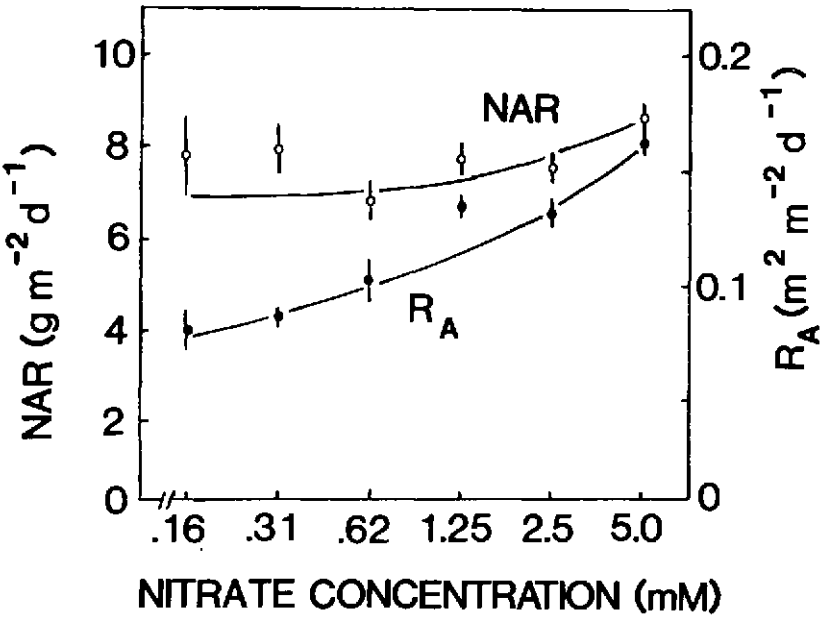

Figure 1. Net assimilation rate (NAR) and relative leaf growth rate (R_A) of cotton plants grown on nutrient solutions containing different concentrations of nitrate. (The data were derived from dry weights [tops only] and leaf areas measured at three weeks and six weeks after germination. Values shown ± standard errors).

from source to sink. Hartt (1970) concluded that in sugarcane, effects of N nutrition on translocation were subsidiary to overall effects on plant growth.

Morton and Watson (1948) and, much later, Radin and Parker (1979a) showed that N effects on leaf area were mediated mostly by differences in leaf cell expansion. This process has recently been studied in more detail in sunflower (Radin and Boyer, 1982). They found that N deficiency markedly decreased plant hydraulic conductivity (ability to transport water from soil to the leaves), thereby increasing the water deficit in the expanding leaves. During the day, when the leaves were transpiring, the water deficit was great enough to lower cell turgor below the critical point for expansion. At night, when transpiration was minimal, cell expansion in N-deficient plants proceeded at almost control rates. Radin and Boyer (1982) also showed that the metabolic aspects of growth ("wall loosening") were unaffected by N deficiency. This means that N metabolism *per se* was not sufficiently altered to have any direct growth consequences.

These surprising data show that N deficiency in sunflower inhibits leaf expansion primarily by altering plant water relations. A very similar conclusion can be reached for cotton, in which N deficiency also decreased hydraulic conductivity (Radin and Parker, 1979a), increased sensitivity of leaf expansion to water stress

(Radin and Parker, 1979b), and inhibited expansion primarily during the daylight hours (Radin, 1983a). Control of cotton leaf expansion by hydraulic conductivity is attractive because it provides a means to explain some otherwise puzzling observations. Radin and Parker (1979b) found strong interactions between temperature and N nutrition on leaf expansion. These data are consistent with effects of temperature on hydraulic conductivity (Markhart *et al.*, 1979a,b) and can be interpreted in such terms.

There are obvious parallels between the effects of N deficiency and the effects of water stress on leaf expansion. In the case of water stress, leaf expansion is inhibited more than photosynthesis (Boyer, 1970; Acevedo *et al.*, 1971). The photosynthate, which normally would support rapid leaf expansion, becomes available for other purposes such as increased root growth (Cutler and Rains, 1977), osmotic adjustment (Turner, 1979), accumulation of starch and other carbohydrates (Ackerson and Hebert, 1981; Ackerson, 1981) and even increased cell wall thickening (Cutler *et al.*, 1977b). Altered partitioning during N deficiency also enhances the root:shoot ratio (Radin *et al.*, 1978), accumulation of starch and other carbohydrates (Medina, 1971; Radin *et al.*, 1978; Wadleigh, 1944; Eaton and Rigler, 1945) and cell wall dry matter (Radin and Parker, 1979a; Shimshi, 1970b). Soluble sugars accumulated in both roots and shoots of N-deficient cotton (Radin *et al.*, 1978). Accumulation of such solutes in the leaves caused a small decrease of about 2 bars in osmotic potential (Radin and Parker, 1979a). These striking similarities between water stress and N deficiency undoubtedly arise because each stress decreases turgor in expanding leaves and thereby inhibits turgor-dependent growth. It is important to note that water stress-induced changes are believed to acclimate plants to further stress (Ackerson and Hebert, 1981; Cutler and Rains, 1977, 1978; Cutler *et al.*, 1977a,b; Radin, 1983b). To the extent that N deficiency parallels water stress, then it too should promote water stress tolerance (Radin and Parker, 1979a). That it does not do so will be discussed later.

RESPONSES TO WATER STRESS

Most experiment stations in the world have some data in their files concerning the interaction of N fertilization and water stress on crop productivity. Some, such as the investigations of Crowther (1934a) in the Sudan, are classic pieces of work. However, little has been done over the years to elucidate some of the basic physiology of these N-water interactions. Our interest in this subject was stimulated by the realization that many developmental effects of N deficiency mimic those of water stress (see preceding section on LEAF EXPANSION AND HYDRAULIC CONDUCTIVITY). Surprisingly, some simple experiments quickly established that N deficiency in cotton causes stomatal closure at abnormally high water potentials (abnormally high plant water status) (Radin and Parker, 1979b). This change is opposite to that caused by water stress acclimation. The most unusual and interesting aspect was that the N-deficient leaves

were not close to wilting when stomata closed. Thus, N deficiency seemed to convert leaves into "water-savers" at the expense of photosynthetic production during a stress cycle. This early stomatal closure was not simply from increased intercellular CO_2 (see earlier PHOTOSYNTHESIS section) but resulted from water stress *per se*, acting through ABA (Radin and Ackerson, 1981).

Data consistent with these observations were reported by McMichael and Elmore (1981) for cotton, Shimshi (1970a) for beans, and Nagarajah (1981) for tea. Similar behavior was found in both sunflowers and soybeans (Radin, unpublished). Ludlow and Ng (1976) reported similar effects in *Panicum maximum* plants grown in controlled environments but not in those grown outdoors.

The importance of this altered stomatal reaction to water stress cannot be overemphasized. The "water-saving" N-deficient plants tend to meter out the available water relatively slowly, thereby prolonging survival considerably after the onset of drought (Radin and Parker, 1979b). This occurs even if the canopy has achieved full cover (Mauney *et al.*, 1982), or if leaf area and soil moisture supply are matched across the N treatments. Furthermore, the slower development of soil moisture stress allows fuller exploration of the soil for stored water. Thus, the trait would seem to have some survival value when water supply is limiting or irregular. Of course, the decreased photosynthesis associated with N deficiency is disadvantageous when water is nonlimiting. These principles are clearly illustrated by Shimshi and Kafkafi (1978). They found that N fertilization greatly decreased stomatal conductance and leaf water potential of dryland wheat, but increased stomatal conductance and only slightly decreased leaf water potential in irrigated wheat. Presumably the fertilized dryland plants had less stomatal control over water loss, and thus quickly reached the point that severe water stress caused stomatal closure. The unfertilized plants, on the other hand, depleted available water more slowly and were less stressed after the same time interval. In the irrigated crop, water stress never developed, and the fertilized plants maintained greater stomatal conductance as described earlier in the section on PHOTOSYNTHESIS. A similar interaction of N and water was seen in the transpiration rates of coffee (Tesha and Kumar, 1978) and tea (Nagarajah, 1981), although water potentials were not reported.

The theoretical complexity of N effects on leaf water potentials can be easily appreciated. On the one hand, N deficiency decreases hydraulic conductivity, a change which would lower leaf water potential when all other factors are unchanged. On the other hand, it promotes early stomatal closure and limits leaf area, changes which tend to increase leaf water potential. Thus, one would expect either positive or negative effects on leaf water potential, depending upon time after last irrigation, evaporative demand, etc. In practice, the change in hydraulic conductivity is frequently overriden by the other effects, even in well-watered crops, and a negative effect of N deficiency on water status of mature leaves is seldom seen (Shimshi and Kafkafi, 1978; Tesha and Kumar, 1978; Nagarajah, 1981).

Another plant reaction to water stress is the senescence and abscission of the lower leaves (Jordan *et al.*, 1972). As with stomatal closure, N deficiency raised the water potential for initiation of senescence (Radin, 1981). However, senescence (or rather the loss of protein and chlorophyll, which represents an advanced stage of senescence) did not seem to be directly related to stomatal closure because the two processes occurred at very different water potentials. In leaf discs, senescence was apparently controlled by variations in both tissue ABA concentration and sensitivity to ABA (Radin, 1981).

INTEGRATION OF NITROGEN EFFECTS

The title of this chapter suggests the existence of specific alterations in plant characteristics which are identified with growth limitation by N. We have examined three such alterations which might underlie the more obvious changes in growth and production, i.e. photosynthesis, hydraulic conductivity, and stomatal sensitivity to water stress. What are the relationships of these three characteristics to each other and to overall crop performance? If there are causal relationships, how might they be useful to an agronomist?

It seems quite clear that photosynthesis per unit leaf area is not nearly as sensitive to N deficiency as the other factors examined. Studies reviewed in the section on LEAF EXPANSION AND HYDRAULIC CONDUCTIVITY point to much earlier effects on leaf growth rate. The accumulation of carbohydrates in N-deficient plants also suggests strongly that excess photosynthate is available for growth. Thus, we feel that decreased photosynthetic rate cannot be the primary deleterious effect of N deficiency. Clearly the factor controlling leaf expansion rate is hydraulic conductivity, and we will examine it in more detail.

The limiting resistance to transpiration flux of water is found in the roots (Kramer, 1969; Graecen *et al.*, 1976; Blizzard and Boyer, 1980). Furthermore, the site of greatest resistance within the root is believed to be in the endodermis or in the stelar parenchyma (see Chapter 3) where water must pass through the membranes of living cells to reach the xylem vessels (Newman, 1974; Graecen *et al.*, 1976). Markhart *et al.* (1979a,b) have presented compelling evidence that a membrane governs variations in hydraulic conductivity (resistance is the reciprocal of conductivity). This conclusion is consistent with data of Oosterhuis and Weibe (1980) who estimated that 76 percent of root resistance in cotton is radial (i.e., in the water pathway between epidermis and xylem vessels) and only 24 percent is axial. It is therefore to be expected that N deficiency, which alters the fatty acid composition of root cell plasma membranes (Rivera and Penner, 1978), should also alter hydraulic conductivity.

Another possible reason for N effects on hydraulic conductivity is raised by work of Richards and Passioura (1981a,b). They showed a marked dependence of calculated root conductivity on the diameter of xylem vessels of wheat roots and a less marked dependence upon number of branches. In sunflower, N deficiency

decreased overall root diameter by 10 percent but had little effect on total root surface area; xylem vessels were not studied but were presumably narrower in N-deficient plants (Radin and Boyer, 1982). The argument that N alters hydraulic conductivity by altering cell size tends toward circularity, in that it requires that the primary event be a change in cell expansion. Changes in cell expansion, on the other hand, have been shown to depend upon hydraulic conductivity, at least in the shoot (Radin and Boyer, 1982; Radin, 1983a). Whether the control of cell expansion in growing roots is fundamentally different from that in shoots has not been addressed.

Interestingly, the N effects on stomatal sensitivity to water stress can also be analyzed in terms of cell membranes. When stomata close, there is concomitant accumulation of ABA in the leaf and secretion of ABA into the apoplast (Ackerson, 1982). However, the accumulation and secretion occur after the stomata are mostly closed (Ackerson, 1982; cf. Trewavas, 1981, for an excellent discussion). Trewavas suggests that changes in guard cell sensitivity to ABA (i.e., changes in the number of ABA receptor sites on the guard cell membranes) control stomatal response. Indeed, Davies (1978) and Ackerson (1980) previously showed that water stress increases stomatal sensitivity to ABA. Lurie and Hendrix (1979) reported that ABA inhibited a plasma membrane ATPase from the epidermis (presumably from the guard cells) of tobacco leaves but had little effect on ATPase activity from the mesophyll membrane preparation. Thus, one seemingly has direct access to the ABA receptor site. This presages rapid progress in understanding environmental effects on stomatal behavior.

What are the agronomic consequences of the N effects described here? One salient feature of the nitrogen stress syndrome is the greater inhibition of growth than of photosynthesis. Presumably the carbohydrates which accumulate could be put to good use supporting yield, so long as the deficiency remains mild. In cotton, this possibility of improved fruiting efficiency under N deficiency has largely been discounted since the work of Eaton and Rigler (1945), and this work therefore bears some detailed examination. Eaton and Rigler grew cotton plants on nutrient solutions containing a series of four nitrate concentrations (1, 4, 16, and 64 mM) ranging from deficient to slightly toxic. Plants were harvested at the time of first boll opening. With increasing N levels, the number of bolls per 100 g fresh weight leaves plus stems (relative fruitfulness) was 6.8, 6.4, 6.4 and 7.6 in open air in the summer, and 4.5, 3.8, 3.4 and 4.1 in a winter greenhouse under a shade. This has long been interpreted to mean that N did not affect relative fruitfulness. However, Eaton (1955) himself viewed the evidence differently because he stated, "Both the high and low nitrate levels depressed growth and increased relative fruitfulness in both tests." He further stated in the same article, "Weight of bolls was less suitable than the number of developing bolls in measuring relative fruitfulness in these tests because of the more determinate growth and higher average weights of the developing bolls in plants on low nitrate at the time the plants were harvested, i.e., only the earliest bolls were retained." This means

that the yield of the low-N plants was set very early; the small advantage in relative fruitfulness shown above would be transformed into a large advantage if only the very early crop were desired.

Wadleigh (1944) also grew cotton plants on a series of four nitrate concentrations and found similar results. Eaton (1955) calculated Wadleigh's relative fruitfulness indexes at 3.6, 3.5, 2.8, and 3.5, going from lowest to highest levels of N.

Radin (unpublished) grew cotton plants on 1 mM (low) or 5 mM (high) nitrate in a greenhouse and followed growth, boll numbers, and partitioning for 139 days after planting. The relative fruitfulness index used by Eaton and Rigler (1945) could not be calculated because fresh weights were not measured. However, number of bolls per unit leaf area provided a similar measure of fruiting efficiency. Table 1 shows that at 75 days after planting, low-N and high-N plants had the same number of bolls, but at 135 days after planting the high-N boll load had increased to three times the boll load of the low-N plants. However, the low-N

Table 1. Boll numbers of upland cotton plants grown on two levels of N nutrition. (Data are means of 12 plants, 6 from each of two cultivars—Acala SJ-4 and Paymaster 909).

Days after planting	Bolls per plant		Bolls per dm^2 leaf area	
	1 mM N	5 mM N	1 mM N	5 mM N
75	2.0	2.1	0.30	0.12
105	2.4	5.3	0.44	0.34
135	3.0	9.3	0.46	0.53

plants were much more efficient in terms of early boll load per unit leaf area. At 75 days after planting the low-N plants carried 2.5 times more bolls per unit leaf area, and the high-N plants did not surpass the low-N plants until 135 days after planting. The fruiting index (boll dry weight as a percentage of total plant dry weight) at 135 days was 41 percent for low-N plants and 27 percent for high-N plants (Table 2). This difference was significant at the 95 percent confidence level. The effects of N on earliness in these experiments are very apparent.

In N-sufficient field plantings in Arizona, the relative fruitfulness at 75 days was 6 to 7 bolls per 100 g fresh weight of stems and leaves (Mauney, unpublished). However, as the plants continued to set bolls and the growth rate was reduced after 75 days, the ratio increased to more than 9 at 100 days. Thereafter, vegetative regrowth reduced the ratio to 6 to 7 at 130 days, after which the ratio increased once again to greater than 9 at 150 days (see Chapter 16).

These two examples from the greenhouse and field show that an index such as relative fruitfulness is not a static quantity during the season. The comparison of low-N and high-N cotton plants therefore depends strongly upon the age and

Table 2. Dry weights and partitioning of cotton plants grown on two levels of N nutrition. (Data are means of 12 plants, 6 from each of two cultivars—Acala SJ-4 and Paymaster 909. Fruiting index is defined as boll dry weight as a percent of total plant dry weight).

Days after planting	Dry weight per plant (g)		Fruiting index (%)	
	1 mM N	5 mM N	1 mM N	5 mM N
68	8.6	21.9	6	3
96	15.3	38.7	34	25
139	24.3	56.8	41	27

yield structure of the crop. For this reason, a single-harvest comparison such as that of Eaton and Rigler (1945) is inadequate. Our presentation of the data shows that low N has little effect on the number of early bolls per plant and improves partitioning of dry matter during that early boll set. However, this advantage in efficiency is lost as the season progresses. Wadleigh (1944) reported very similar results.

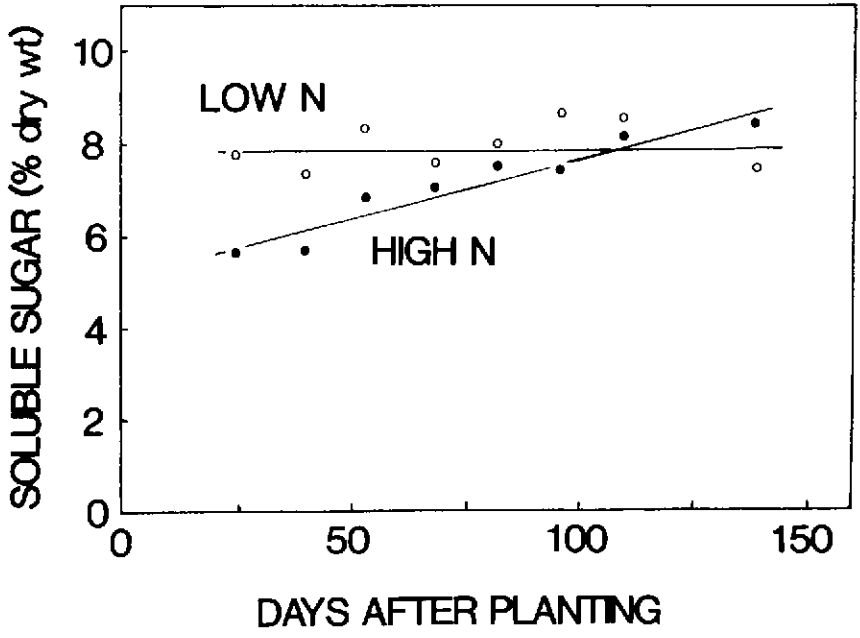

Figure 2. Soluble sugar concentrations in stems plus leaves of the cotton plants described in Tables 1 and 2. (Sugars were determined colorimetrically with the phenol-H_2SO_4 test against glucose as the standard).

Table 3. Fruiting sites and boll retention at each fruiting branch node of plants grown on three levels of N. (Data are from Table 17 of Wadleigh, 1944. Wadleigh's designations of series A, B and D correspond to 0.56, 1.7 and 15.6 mM NO_3N in the nutrient solution, respectively).

Treatment	Fruiting branch node					Total
	1	2	3	4	5	
A						
Flowers/plant	10.0	6.9	3.0	0.3	0	20.2
Bolls/plant	4.7	0.6	0	0	-	5.3
% Retention	47	9	0	0	-	26
B						
Flowers/plant	13.7	10.2	6.8	2.1	0.2	33.0
Bolls/plant	7.2	2.3	0.6	0	0	10.1
% Retention	53	23	9	0	0	31
D						
Flowers/plant	18.9	14.6	12.3	8.1	2.5	56.4
Bolls/plant	11.4	5.9	4.3	1.5	0	23.1
% Retention	60	40	35	19	0	41

Plants from the greenhouse experiments described earlier (Table 1) were analyzed for soluble carbohydrates. During the vegetative stage of growth, low-N plants contained considerably higher concentrations of soluble carbohydrates than high-N plants. By about 110 days after planting, however, their positions had become reversed as the early fruit load quickly drained the smaller low-N plants of their reserves (Figure 2). This inability to support all the sinks suggests that N deficiency should also increase shedding. Plant maps of Wadleigh (1944) support this deduction. Nitrogen deficiency slightly increased the percent shed at the first nodes of fruiting branches and drastically increased the percent shed at all subsequent nodes (Table 3). In terms of flower production and boll shedding, the second node of severely N-deficient plants (series A) closely resembled the third node of moderately deficient plants (series B) and the fourth node of N-sufficient plants (series D). Both plant size (number of fruiting positions) and shedding contributed about equally to the change in boll number per plant.

We have also observed that low N greatly suppresses fruiting branch development (Radin and Mauney, unpublished). This suppression resembles the cessation of growth typically observed in high-N plants, except that it occurs much earlier. The similarities in growth and shedding patterns suggest that even in "N-sufficient" plants, limitation of branch length and reduced boll retention at distant nodes along fruiting branches may be from localized N stresses caused by N partitioning among competing growth centers.

The developmental effects of N nutrition are summarized in Table 4. From this table, derived from Wadleigh (1944) and from this chapter, one can draw the

following useful generalization: N nutrition does not alter morphogenetic patterns. Examples of morphogenetic characters include node of first flower (also

Table 4. Summary of effects of N nutrition on growth and development of cotton plants.

CHARACTERISTICS AFFECTED BY N
1. Growth Rate
2. Leaf Area
3. Earliness
4. Boll Shedding
5. Seed and Lint Weight per Boll
6. Stomatal Response to Water Stress
CHARACTERISTICS NOT AFFECTED BY N
1. Node of First Flower
2. Node of First Open Boll
3. Flowering Interval
4. Seeds per Boll

time to first flower), flowering interval (both horizontal and vertical), etc. Nitrogen nutrition does alter processes which depend upon partitioning of assimilates. Examples of this type of character include growth rates of leaves and stems, boll shedding, seed and lint weight, etc. The lone response to N which does not obviously fit this pattern is stomatal response to water stress. Preliminary data (Radin, unpublished) suggest that even this response may depend upon leaf carbohydrate levels. If this suggestion should be true, then stomatal behavior would also fit the generalization.

PROSPECTS FOR CROP IMPROVEMENT

Clearly N deficiency has several consequences, some of which can be advantageous and some of which can be disadvantageous. By limiting leaf area, slowing growth, and increasing stomatal sensitivity to water stress, N deficiency increases drought resistance (drought avoidance in the terminology of Levitt, 1972.) Because cotton is ancestrally a desert perennial, this effect of N presumably once had ecological significance—especially because desert soils are typically low in organic matter and N (West and Klemmedson, 1978). The induced drought avoidance may similarly have significance in areas of dryland culture where chronic water stress prevents attainment of the yield potential. Peterschmidt and Quisenberry (1981) identified a drought-avoiding genotype of cotton. It was superior to other genotypes in dry matter production under dryland conditions but was inferior under irrigation (Quisenberry *et al.*, 1981). It is therefore relevant

that N applications across the Cotton Belt vary with the degree of water stress expected, with much more N applied in the irrigated West than in the dryland areas of west Texas and Oklahoma (Tucker and Tucker, 1968).

The problem for an agronomist or a plant breeder is to add N to support yield, yet retain the benefits of low N on efficiency and drought avoidance. It may be possible to select for enhancement of individual characters of the N stress syndrome. The drought-avoiding genotype of Peterschmidt and Quisenberry (1981) is a good example, assuming that the selection was not inadvertantly based upon differences in N status of the plants. Quarrie (1980) has also found genetic differences in drought avoidance of wheat based largely upon differences in root-shoot ratio. In corn, hydraulic conductivity has been shown to be genetically controlled (Dube *et al.*, 1975; Harris and Heath, 1981). Passioura (1972) showed that wheat plants with decreased hydraulic conductivity were better able to conserve soil moisture until grain filling. Thus, this character may be equal in importance to stomatal responses in improving dryland performance.

Altered cultural practices might also improve the suitability of a plant for its environment. Based on the preceding discussion, it seems logical that late applications of N (starting perhaps at first flower) might partially separate the positive effects of N on yield from the negative effects on drought resistance. Gardner and Tucker (1967) studied timing of N applications in irrigated cotton in Arizona. They found that late or split applications tended to increase yields even though plant size, number of flowers, and number of bolls tended to be slightly less. Recent emphasis on water conservation by withholding irrigation water during vegetative growth (Guinn *et al.*, 1981) would make timing of N applications even more critical than previously suggested. A movement toward short-season cotton for reasons of integrated pest management (Mauney *et al.*, 1972) would also emphasize the need for efficiency in the early fruiting period. Other approaches to control of N fertilization, e.g., slow-release fertilizers, combinations of conventional and slow-release fertilizers, or even foliar fertilization, have not yet been carefully explored.

SUMMARY

Low nitrogen fertility is associated with several alterations of crop development in cotton (*Gossypium hirsutum* L.), including slower growth and smaller leaves, greater root:shoot ratio, increased earliness, greater shedding percentage, and increased drought resistance. We have identified three basic physiological responses of cotton plants to low nitrogen fertility which underlie all these effects. These three (collectively called the nitrogen stress syndrome) are: (1) decreased photosynthetic rate; (2) decreased hydraulic conductivity; and (3) increased stomatal sensitivity to water stress. Decreased hydraulic conductivity severely limits growth, allowing reserve carbohydrates to accumulate before flowering despite the lowered photosynthesis. These reserve carbohydrates are utilized

during early boll set but soon become depleted. Thus, the late yield is largely lost from N-limited plants as a result of the low photosynthetic rate. Increased stomatal sensitivity to water stress tends to promote a "water-saving" mode of drought avoidance in N-limited plants, leading to better acclimation to dryland conditions (where yield limitation by N is unimportant because of the greater yield limitation by water). Recognition of the basic physiological mechanisms underlying field behavior may allow enhancement of drought resistance and earliness, either by improved management of nitrogen fertility or by genetic selection for altered physiological responses to nitrogen.