Integrated Responses of Plants to Stress

A centralized system of physiological responses

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I n both natural and agricultural communities, the environment is seldom optimal for plant growth. Environmental stress limits the overall productivity of US agriculture to 25% of its potential (Boyer 1982). All mesic environments experience large seasonal fluctuations in light, moisture, temperature, and nutrients, often to levels that are suboptimal for plant growth, so the plant is continuously encountering new combinations of environmental stresses. Moreover, most natural environments are continuously suboptimal with respect to one or more environmental parameters, such as water or nutrient availability.

The nature of controls over plant growth in suboptimal environments is of particular interest, because these are the only habitats into which agriculture can expand in most developing countries, and impending global climate change will alter the suitability of most terrestrial habitats for plant growth. Consequently, we need to understand the physiological mechanisms that enable plants to survive and reproduce under suboptimal conditions.

To date, most research on the physiological responses of plants to environmental stress has focused on the responses of plants to specific stresses (Osmond et al. 1987). For example,

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All plants respond to stress of many types in basically the same way

plants adjust osmotically in response to salt and water stress (Morgan 1984), increase their potential to absorb nutrients in response to nutrient stress (Lee 1982), and alter the quantity and balance of photosynthetic enzymes in response to shade or light stress (Evans 1989).

However, two lines of research suggest that plants also have a centralized system of stress response that enables them to respond to any physiological stress, regardless of the nature of that stress. First, ecologists have noted that certain suites of traits characterize plants from all low-resource environments (e.g., deserts, tundra, shaded understory, and infertile soils). These traits include slow growth, low photosynthetic rate, and low capacity for nutrient uptake (e.g., Chapin 1980, Grime 1977, Parsons 1968).

Second, physiologists have observed that individual plants respond to most environmental stresses by changing their hormonal balance, frequently producing more abscisic acid and often less cytokinins (e.g., Chapin et al. 1988b). Recent research suggests that these hormonal changes are the trigger that directly elicits reduced growth in response to environmental stress; low availability of a resource simply activates this stress-response
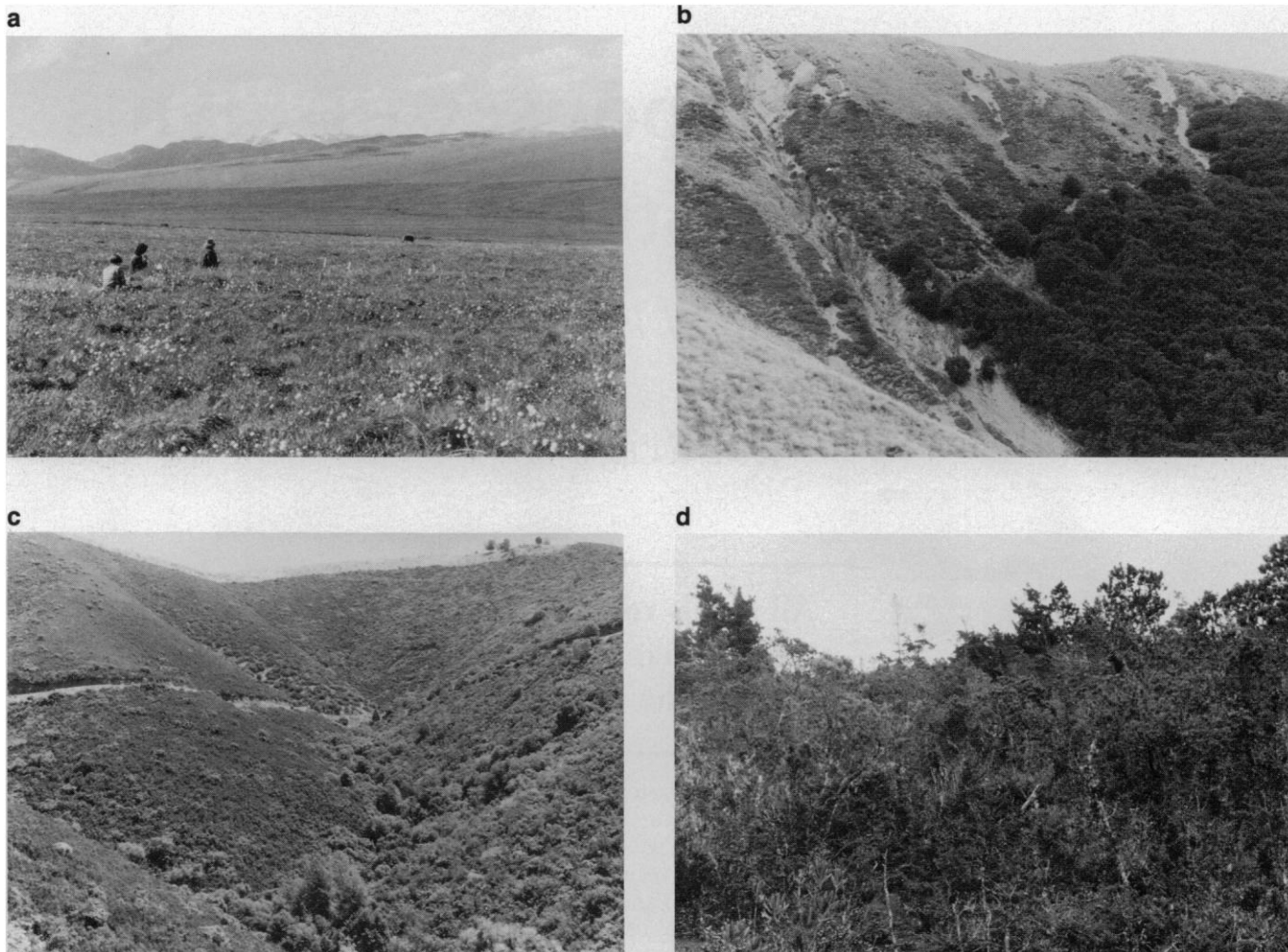
system.

The purpose of this article is to summarize and integrate these two lines of research and to propose that there is a basic physiological framework that regulates plant growth in response to environmental stress. This framework is complex, involving changes in hormonal balance, water relations, carbon balance, and nutrient use. Broad multidisciplinary approaches may now provide new insights into plant responses to environmental stress. This idea contrasts with the general trend in plant physiological research toward increasing biochemical detail of specific physiological processes. I emphasize the response of barley to nutrient stress as an example of the integrated nature of carbon, water, nutrient, and hormonal balances of plants.

Traits common to plants in low-resource environments

The central feature of plants adapted to low-resource environments is that they grow slowly, even when provided with an optimal supply and balance of resources. This slow growth is seen in plants that are adapted to infertile soils (Chapin 1980, Clarkson 1985), dry or saline environments, or deep shade (Grime 1977, Parsons 1968). Associated with this slow growth is a low capacity to acquire certain resources. Plants from infertile soils have a low capacity to absorb phosphate (but not nitrogen; Bloom 1985) and to photosynthesize (Chapin 1980). Similarly, understory and many desert plants have an inherently low photosynthetic potential

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Plants growing in stressed conditions. (a) Alaskan tussock tundra, which is limited primarily by temperature and nitrogen. (b) New Zealand tussock grassland, which is limited primarily by phosphorus. (c) California chaparral, which is limited primarily by moisture. (d) California pygmy forest, which is limited primarily by nutrients. The two grass communities have a similar structure, despite the fact that they experience quite different environmental stresses.

(Caldwell 1985, Sims and Pearcy 1989). There are at least three physiological mechanisms that could explain the slow growth of low-resource-adapted plants.

First, the slow growth even under optimal conditions may reflect a low capacity to capture resources. Plants from infertile soils are often relatively inflexible in root:shoot ratio and may allocate insufficient biomass to leaves under high-nutrient conditions to acquire sufficient photosynthate to grow rapidly (Chapin et al. 1982). Moreover, as described above, plants from low-resource environments often have a low physiological capacity to acquire resources per gram tissue.

Second, plants from low-resource environments may allocate fewer resources to growth because of propor-

tionally greater allocation to functions that improve survivorship in harsh environments (Mooney and Gulmon 1982). Plants grow exponentially in weight as long as they allocate new biomass to organs, such as leaves and roots, that increase the plant's capacity to acquire resources. Plants that divert resources to functions other than growth (e.g., to defense or storage) will grow more slowly than individuals that allocate only to resource-acquiring functions.

Chemical defenses against pathogens and herbivores are most strongly developed in species adapted to low-resource environments such as infertile soils, deep shade, and drought (Bryant et al. 1983, Coley 1983). In these environments, plants are less able to acquire resources necessary to

replace tissues lost to herbivores (Bryant et al. 1983) and because a given amount of tissue loss represents a larger proportion of the productive capacity of the plant (Coley et al. 1985).

Similarly, storage is well developed in perennial plants that occupy low-resource environments both as insurance against catastrophic tissue loss and as a support for rapid growth during brief periods when conditions are favorable (Chapin et al. 1990). Annuals, which allocate relatively few resources to storage or defense, show no consistent pattern of growth rate with respect to environment (Chapin et al. 1989). Thus there is good evidence that differences in allocation to growth versus nongrowth functions explain why many perennial plants

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from harsh environments grow slowly.

Third, plants from low-resource environments may grow slowly because of internally imposed constraints on growth. Perhaps these plants produce less of the growth hormones or are less sensitive to growth hormones. This possibility has, to my knowledge, not been explored. However, it seems reasonable, because plants from infertile soils maintain higher tissue nutrient concentrations than rapidly growing, high-nutrient-adapted plants under nutrient-limiting conditions (Chapin 1980, Chapin et al. 1982), suggesting that the low-resource plants are not growing to the absolute limit of their tissue nutrient supply. Similarly, shade plants maintain higher tissue carbohydrate concentrations under deep shade than do plants adapted to high light.

Regardless of the mechanisms responsible for the slow growth of plants from low-resource environments, it is clear that these species share a common suite of physiological traits such as slow growth, low potential for resource capture, effective chemical defense, and a well-developed capacity for reserve storage. This observation implies a common physiological basis for slow growth, despite its evolution in response to quite different selective forces.

A centralized mechanism of stress response

Growth response to nutrients. A common perception is that plant response to insufficient nutrient supply involves physiological changes that are unique to nutrient stress. However, the nutritional response of plants exhibits many features that are similar to responses of plants to other environmental stresses.

NUTRIENT UPTAKE AND MOBILIZATION. When deprived of external nitrogen supply, barley plants increase their potential to absorb nitrogen as measured per gram of root (Figure 1). This change is also observed in most other plants tested (Harrison and Helliwell 1979, Lee 1982). The increased absorption potential with nitrogen stress probably reflects a change in the quantity or activity of ion-specific carriers in the plasma
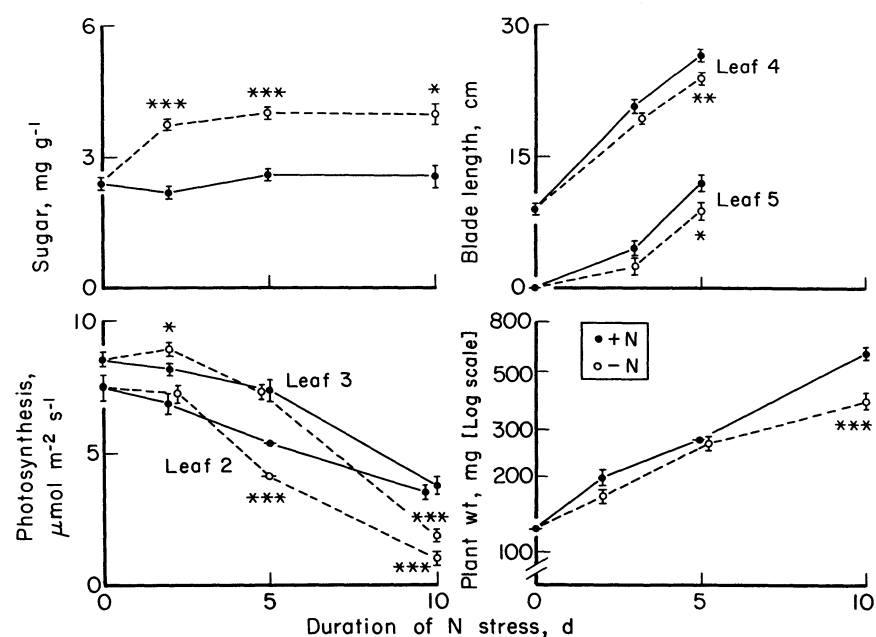

Figure 1. Nitrate absorption rate (measured under standard conditions), root:shoot ratio, and nitrate and organic nitrogen concentrations of old leaves of barley grown with 10 mM nitrate (filled circles) and without nitrate (open circles). Data are means ± SE, expressed per gram fresh weight (Chapin et al. 1988a, 1988b). Significant differences from control at $p < 0.05$, 0.01, and 0.001 are indicated by *, **, and ***, respectively.

membrane of roots (Glass 1983). Plants also rapidly increase their proportional allocation to root growth in response to inadequate nutrient supply (Figure 1; Brouwer 1966). The

physiological mechanism by which allocation is altered remains unclear. However, it is probably more complex than Brouwer's (1966) hypothesis that the organ closest to the
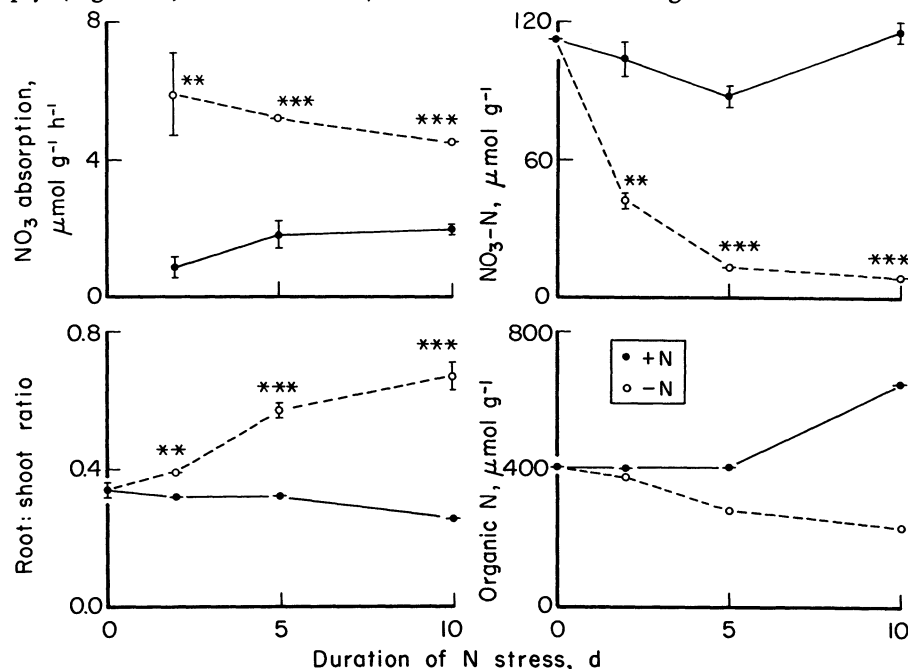

Figure 2. Sugar concentration in roots, photosynthetic rate of old leaves, lengths of leaf 4 and 5, and total weight of barley plants grown with and without nitrate (Chapin et al. 1988b). Statistics as in Figure 1.

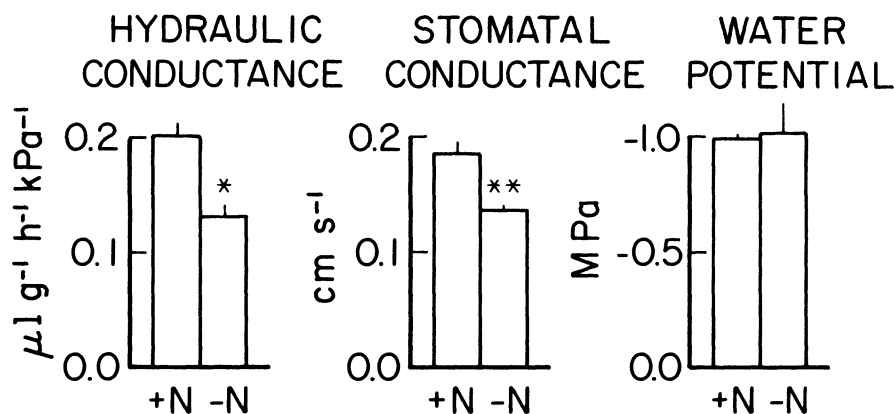## HYDRAULIC CONDUCTANCE   STOMATAL CONDUCTANCE   WATER POTENTIAL

Figure 3. Root hydraulic conductance, stomatal conductance of old leaves, and water potential of young leaves of barley at the time (day 3) that growth begins to decline after removal of nitrogen supply (Chapin et al. 1988b). Statistics as in Figure 1.

growth-limiting resource (roots in the case of nitrogen stress, shoots in the case of carbon stress) has first access to the growth-limiting resource. Hormone balance is probably involved (Jones et al. 1987).

A second major mechanism for maintaining growth rate in the face of incipient nutrient deficiency is a withdrawal of tissue nitrogen stores, particularly from old leaves. Barley has high vacuolar nitrate concentrations (22% of total nitrogen in old leaves of plants grown under optimal nitrogen supply). These tissue nitrate reserves are drawn down rapidly in response to inadequate external supply of nitrogen (Figure 1). However, the nitrate stores are not large enough, nor can they be mobilized rapidly enough (60% of the total nitrate reserve in two days), to meet the nitrogen needs of the plant growing at a maximal rate for more than a few hours. Therefore, organic nitrogen is also withdrawn from old leaves under conditions of nitrogen stress, presumably through breakdown of a wide variety of photosynthetic and nonphotosynthetic proteins (Evans 1989) and through declines in rate of protein synthesis under conditions of nitrogen stress (Cooke et al. 1979). Similar mobilization of nitrogen stores to buffer plants from incipient nitrogen stress is found in most species studied (Chapin 1980).

PHOTOSYNTHESIS. Photosynthetic rate correlates closely with leaf nitrogen content in barley and other species (Chapin et al. 1988b, Evans 1989, Field and Mooney 1986), pre-

sumably because a low nitrogen supply results in a low concentration of photosynthetic enzymes, which in turn causes a low rate of photosynthesis per gram of leaf. However, nitrogen stress also causes a decline in stomatal conductance, which could also explain the decline in photosynthesis. In most plants, stomatal conductance and photosynthetic potential are so closely matched that both parameters simultaneously limit photosynthetic rate (von Caemmerer and Farquhar 1981).

Photosynthetic potential probably drives stomatal conductance. The ev-

Figure 4. Abscisic acid concentration of leaves of barley grown with (O) and without (●) nitrate (Chapin et al. 1988b).

idence is that the CO_2 concentration inside the leaf tends to be high under conditions of insufficient nitrogen supply, indicating that stomates are relatively open and that photosynthetic potential is the primary limitation on photosynthetic rate (Evans 1983, von Caemmerer and Farquhar 1981, but see Chapin et al. 1988b). On the other hand, there is a low rate of photosynthesis per unit of nitrogen in plants with low tissue nitrogen concentrations, indicating that either much of the nitrogen present in a low-nitrogen leaf is not involved in photosynthesis or that some other factor (e.g., stomatal conductance) tends to limit photosynthesis under these conditions (Field and Mooney 1986).

GROWTH. There are several lines of evidence suggesting that a low photosynthetic potential per gram of leaf does not directly cause the slow growth of nitrogen-limited plants. First, plants whose growth is nitrogen-limited always have high concentrations of carbohydrates (Figure 2; Brady 1973, White 1973), suggesting that it is not the availability of photosynthate that directly restricts growth under conditions of nitrogen limitation. Second, in barley and other species (Radin and Eidenbock 1986), the decline in leaf growth rate due to nutrient limitation preceeds the decline in total plant weight gain. Third, in barley, leaf growth declines before there is a major change in photosynthetic rate of young leaves (i.e., those that provide most carbon to support continued shoot growth; Rawson et al. 1983). Therefore, to the extent that nitrogen effects on photosynthesis are important, they probably act initially through effects on leaf weight and quantity of photosynthetic tissue (a consequence of changing growth and allocation) and on source-sink interactions, which govern demand for carbohydrate, rather than through direct effects on photosynthetic potential per gram of leaf.

Changes in plant-water relations have been suggested as the physiological mechanism by which nitrogen limitation causes a reduction in growth (Radin 1983, Radin and Boyer 1982). Even in hydroponic systems, where water availability to plants is unlimited, nitrogen stress quickly causes a decline in hydraulic conductance of roots (and therefore
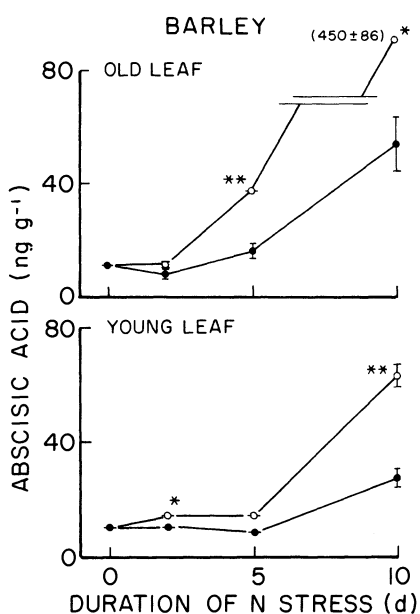
water uptake) and an associated decline in stomatal conductance (and therefore transpirational water loss; Figure 3). In some cases, particularly in plants grown under high irradiance, plant water potential declines in response to nitrogen stress because root hydraulic conductance is more sensitive to nitrogen stress than is stomatal conductance (Radin and Boyer 1982). In such situations, decreased turgor may be one mechanism by which leaf growth is inhibited. In other cases, the changes in water uptake and loss are in balance, with no net change in plant water potential (Figure 3).

Thus, although nitrogen stress causes substantial reduction in water uptake and loss, the resulting changes in tissue water relations are not necessarily the direct cause of the decline in leaf growth. Because at least two mechanisms allow nutrient stress to reduce growth rate, there is redundancy, ensuring that the plant will respond sensitively to its environment.

The water relations of expanding cells, not the water relations of mature tissues (which most plant researchers, including myself, have measured), are important in controlling growth (Boyer et al. 1985, Michelena and Boyer 1982). Nonetheless, patterns of water potential in expanding cells often correlate with patterns in entire leaves or in adjacent mature leaves when plants exposed to different degrees of water stress are compared (Barlow 1986). I cannot preclude the possibility that nitrogen stress reduces growth by reducing turgor of expanding cells, but current evidence suggests that there are also other mechanisms by which nitrogen stress reduces the rate of plant growth.

HORMONAL BALANCE. Insufficient nitrogen supply consistently results in an increase in abscisic acid (ABA) in leaves (Figure 4; e.g., Chapin et al. 1988b, Radin et al. 1982). The decline in stomatal conductance caused by ABA (Schulze 1986) could be part of the mechanism by which photosynthesis declines with nitrogen stress (Figures 2, 3).

ABA content of roots may decrease (Angelova and Georgieva 1983, Ansimov and Bulatova 1982, Safarlieva et al. 1979), increase, or remain un-
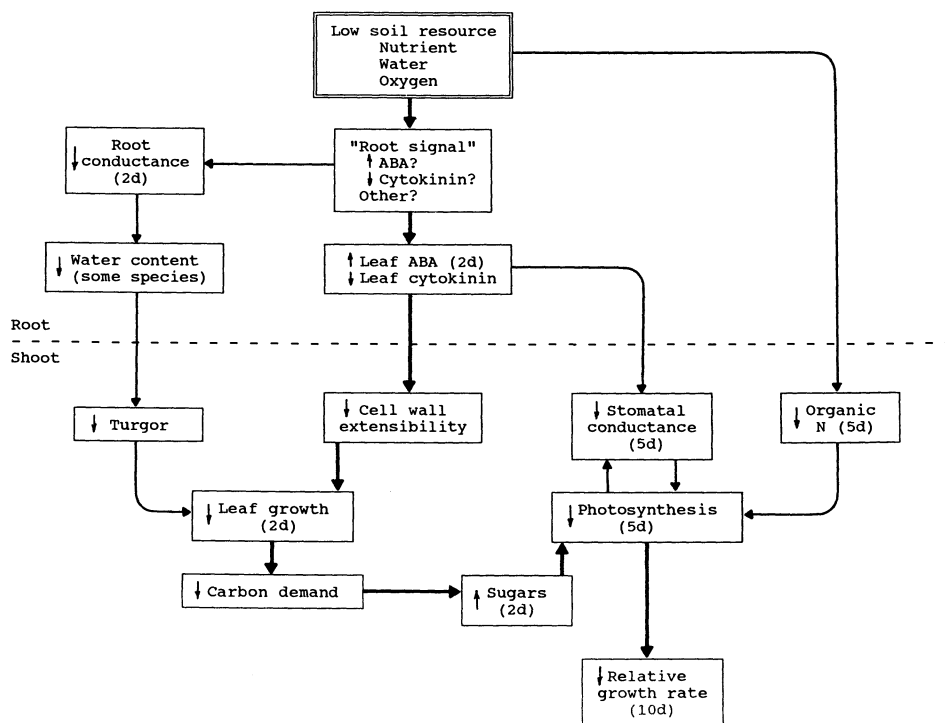

Figure 5. Proposed network of cause-and-effect relationships linking low nitrogen availability with slow growth. Time after removal of nitrate is shown in parentheses.

changed (Chapin et al. 1988a) in response to low nitrogen supply. ABA causes a large increase in hydraulic conductance of roots (Chapin et al. 1988a, Ludewig et al. 1988), so any decrease in root ABA in response to nitrogen stress could explain the decline in root hydraulic conductance in nitrogen-stressed plants.

A decline in leaf growth could reflect slower cell division or enlargement. Normally, cell enlargement is affected earlier and to a greater degree by nitrogen stress than is cell division (Milthorpe and Moorby 1974). A decline in cell enlargement, in turn, could reflect either a change in turgor, a change in the resistance of the cell wall to expansion (yield threshold), or a change in cell wall extensibility (Cleland 1986). ABA is known to reduce cell wall extensibility (Van Volkenburgh and Davies 1983) and could explain the observed changes in leaf growth (Quarrie and Jones 1977, Watts et al. 1981). Cytokinins also tend to decline under conditions of low nitrogen supply and could be involved in controls over cell division and expansion.

THE MECHANISM. I suggest the following scenario as a possible mecha-

nism by which insufficient nitrogen supply leads to reduced growth (Figure 5). Insufficient nitrogen supply triggers a change in hormonal balance, including an increase in leaf ABA. The increase in leaf ABA reduces cell wall extensibility and therefore causes a decline in leaf elongation. Alternatively, in some plants the altered hormonal balance could reduce root hydraulic conductance, reduce turgor, and thereby reduce leaf growth. Regardless of the mechanism by which it is achieved, the decline in growth reduces the demand of the plant for carbon, so carbohydrates accumulate and photosynthesis declines to match the lower requirement of the plant for carbohydrate. The mechanisms by which photosynthesis declines probably include ABA-induced decline in stomatal conductance (Schulze 1986) and decline in concentrations of photosynthetic enzymes (Evans 1989). Thus the decline in leaf elongation and carbon requirement probably lead to the decline in photosynthesis, rather than the other way around.

Why should plants devise an elaborate hormonal mechanism to reduce growth if direct nitrogen effects on
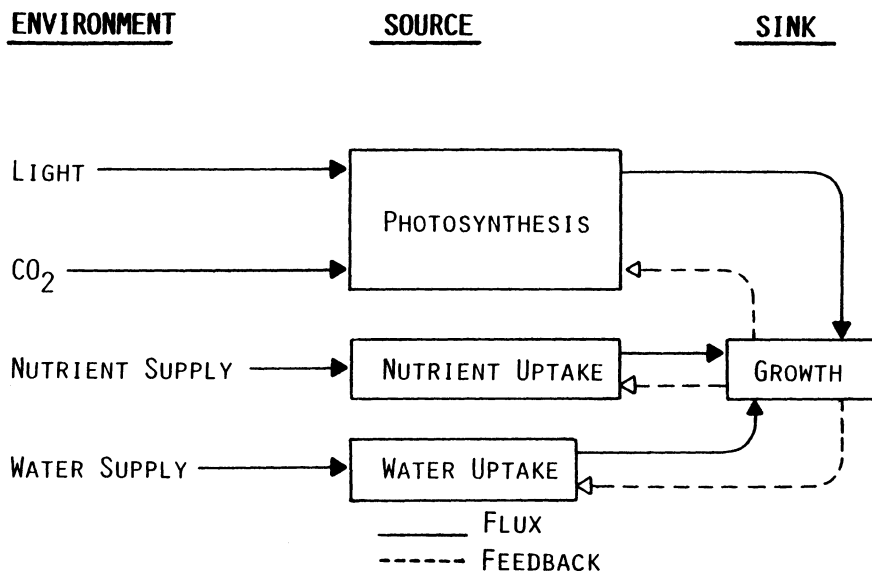
Figure 6. The direct environmental controls and source-sink feedbacks affecting resource acquisition and growth by plants.

stressed plants, presumably because of a decline in nutrient demand. Concentrations of photosynthetic enzymes decline in response to drought, as does photosynthetic rate (Kluge 1976).

There are, however, two observations suggesting that this decline in photosynthesis is not directly responsible for drought-induced growth declines. First, mild drought stress causes carbohydrate concentrations to increase (Hsiao et al. 1976). Second, the decline in leaf growth preceeds the decline in dry weight accumulation (Munns et al. 1982, Wardlaw 1969). Together these observations indicate that drought causes a reduction in growth most directly by altering hormonal balance, but that associated with this decline in growth are interconnected changes in plant nutrition, carbon balance, and water relations.

Growth response to flooding stress. As with nutrient stress and drought, water-logging causes an increase in ABA that could be responsible for changes in growth (Wadman-van

concentrations of photosynthetic enzymes would eventually do the same job? Perhaps the rapid effects of incipient nitrogen stress on leaf elongation (acting through altered turgor and/or cell wall extensibility) serve as an early warning system that enables the plant to reduce growth and change patterns of allocation before there is a severe imbalance of carbon- and nitrogen-containing metabolites. By maintaining a balance between carbon and nitrogen reserves, plants minimize the cost of growth (Bloom et al. 1985).

Growth response to water stress. Recent studies suggest that water stress and osmotic stress cause a reduction in growth through basically the same mechanism implicated above for nutrient limitation. They cause a decrease in cytokinin transport from roots to shoots and/or an increase in leaf ABA; these changes in hormone balance cause changes in cell wall extensibility and therefore growth (Blackman and Davies 1985). In experiments where root pressure chambers or split-root systems are used to maintain a constant leaf turgor, drought still causes a decline in leaf growth (Blackman and Davies 1985, Matthews et al. 1984, Michelena and Boyer 1982, Schulze 1986, Termaat et al. 1985; but see Neumann et al. 1988). Thus drought causes a reduction in leaf growth through a hormonal signal from roots and not

through a direct effect of turgor on cell enlargement.

As with nutrient stress, water and salinity stress cause changes in virtually all physiological systems in the plant. Potential of roots to absorb nutrients generally declines in water-
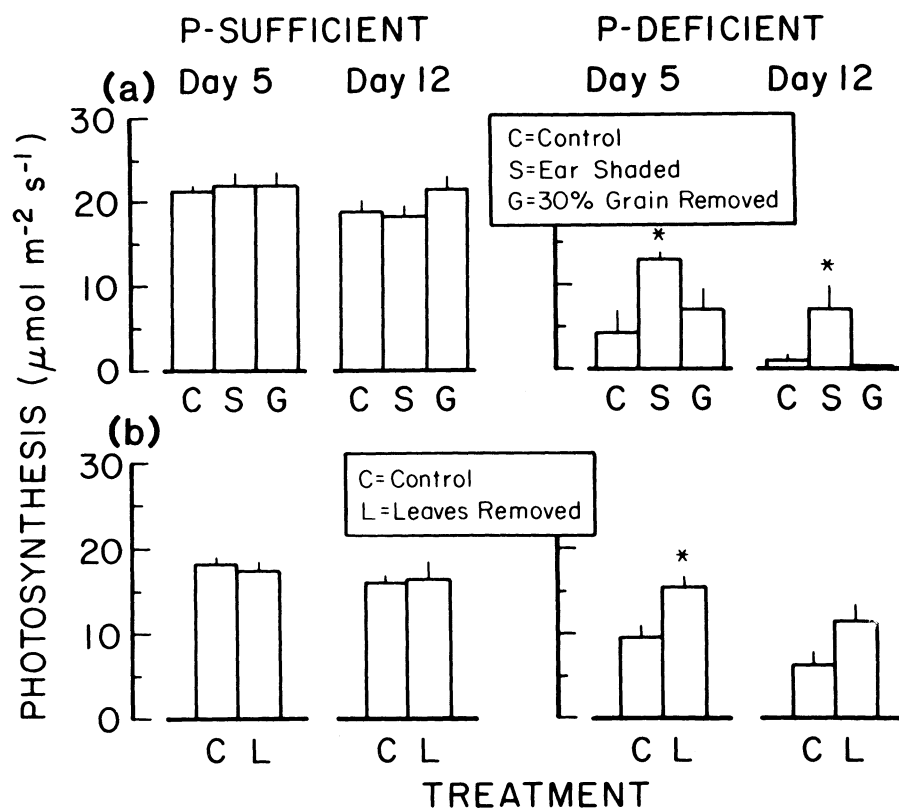

Figure 7. Photosynthetic rate in response to phosphorus deficiency and manipulation of sink strength (Chapin and Wardlaw 1988). Statistics as in Figure 1.

Schravendijk and van Andel 1985). As with other stresses, growth is inhibited at the same time that ABA increases but before there are detectable changes in water or nutrient status of plants. After the reduction in growth rate, there are decreases in potential to absorb nutrients, concentrations of photosynthetic enzymes, rate of photosynthesis, root hydraulic conductance, tissue water potential, and turgor (Wadman-van Schravendijk and van Andel 1985). These observations suggest a syndrome of physiological responses quite similar to that described for plant responses to other stresses.

Physiological integration

A single common mechanism by which plants respond to diverse environmental stresses may explain how stress reduces plant growth, but it does not explain how plants reduce their rate of acquisition of other nonlimiting resources to maintain a reasonable balance of internal resources. Theoretical arguments based on economic analogies suggest that plants minimize the cost of growth if allocation is adjusted such that all resources are equally limiting to growth (Bloom et al. 1985). In other words, under conditions of nutrient limitation, plants should restrict carbon gain, and under low-light conditions plants should restrict nutrient uptake (Figure 6). Consequently, for resources that do not directly limit growth, the plant demand for resources (sink strength) should be more important than resource availability in the environment in determining the rate of resource acquisition (source activity).

Nitrogen limitation of plant growth provides support for this hypothesis. Under conditions of high nitrogen availability, plants have a low potential to absorb nitrogen (Figure 1) and a low allocation to roots (Figure 3). Under these circumstances, nitrogen demand by the plant has more effect on nitrogen uptake than does nitrogen availability in the soil (Clarkson 1985). By contrast, when growth is nitrogen-limited, nitrogen uptake is controlled by the rate of supply from the soil. Under conditions of low nitrogen availability, there is a decline in leaf allocation, photosynthesis (Figure 3), and water uptake (Figure 4), due to decreased

demand by the plant. Similar patterns are observed in most other studies (Chapin 1980, Clarkson 1985). However, plants do not compensate perfectly. Nitrogen-limited plants have high carbohydrate status (Figure 3), and light-limited plants have high tissue-nitrogen concentrations (Evans 1989).

Only experiments can provide a true test of the hypothesis that source-sink interactions control acquisition of nonlimiting resources. Experiments with the flag leaf (a well-defined source of carbon) and the developing grains (a well-defined sink for carbon) of barley provide one such test. The photosynthetic rate of phosphate-deficient barley plants was increased by manipulations that increased plant demand for carbohydrates (shading of the ear or removal of other leaves; Figure 7). Similarly, small flag leaves (i.e., those having large sinks relative to their own size) had high rates of photosynthesis (Chapin and Wardlaw 1988); this relationship was most pronounced under conditions of phosphate deficiency. In other words, source-sink interactions controlled photosynthesis most strongly under nutrient-limiting conditions.

Conclusions

The results described suggest that all plants respond to environmental stress in basically the same way: through a decline in growth rate and in the rate of acquisition of all resources. These same traits are observed in species that have adapted evolutionarily to low-resource environments and in any plant that has adjusted physiologically to a low resource supply.

It appears that plants exhibit a centralized system of stress response that can be triggered by a diverse range of stresses. This centralized stress response system is hormonally mediated but involves integrated changes in nutrient, water, carbon, and hormonal balances of plants. Further studies of these stress responses should consider the integrated nature of these different systems rather than focusing on a single environmental resource. This integration will require a broad interdisciplinary approach that draws on the skills of many types of physiologists and ecologists.

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