



D`Ubh`F YgdcbgYg`hc`A i`h]d`Y`9bj]f cba YbhU` : UWcf g
5 i h\ cf fyt : "" Ghi Uf h`7\ Ud]b` ==z` 5 f bc`X` >"" 6`cca ž`7\ f]ghcd\ Yf`6"" :]Y`Xž`F]WU`X` <"" K Uf]b[
Gci fW. : 6]cGVYbWZ`J c`"" +ž`B c`""ž` <ck` D`Ubhg`7cdY. D`Ubh`D\ mg]c`c[]WU`9Vt`c[m`f] Ub`ž`% , +ž`
dd"" (-!) +
Di V`g\ YX`Vm`5a Yf]Wb`-bgh]hi hY`cZ`6]c`c[]WU`GVYbWg
GhU`Y`I F @ : <http://www.jstor.org/stable/1310177>
5 VWggYX. : \$) # \$' # & \$ \$-`%) . (\$

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=aibs>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



American Institute of Biological Sciences is collaborating with JSTOR to digitize, preserve and extend access to BioScience.

<http://www.jstor.org>

Plant Responses to Multiple Environmental Factors

Physiological ecology provides tools for studying how interacting environmental resources control plant growth

F. Stuart Chapin III, Arnold J. Bloom, Christopher B. Field, and Richard H. Waring

Most plants require a similar balance of resources—energy, water, and mineral nutrients—to maintain optimal growth. Natural environments, however, differ by at least two orders of magnitude in the availability of these resources. Light intensity varies 100-fold from the canopy to the floor of a rainforest (Björkman 1981); annual precipitation ranges 500-fold (10–5000 mm/yr) from deserts to tropical rainforests; and the amount of nitrogen available to plants varies from 0.09 g/m² · yr in polar desert (Dowding et al. 1981) to 22.8 g/m² · yr in a rich tropical rainforest (Vitousek 1984). Plants growing in these diverse environments maintain tissue concentrations of organic carbon, water, and to some extent nutrients within fairly narrow limits. How do plants compensate so successfully for these dramatic differences in resource availability?

Elucidating plant responses to resource imbalance requires a multidisciplinary approach. The study of resource availability falls in the provinces of community or ecosystem

Chapin is a professor in the Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99701. Bloom is an assistant professor in the Department of Vegetable Crops, University of California, Davis, CA 95616. Field is a staff scientist in the Department of Plant Biology, Carnegie Institution of Washington, Stanford, CA 94305. Waring is a professor in the School of Forestry, Oregon State University, Corvallis OR 97331. © 1987 American Institute of Biological Sciences.

How do plants compensate so successfully for dramatic differences in resource availability?

ecology, micrometeorology, and soil science. The metabolic and structural bases of plant responses falls within the realms of physiology, biochemistry, and functional anatomy. Plant physiological ecology borrows heavily from all these disciplines to concentrate on the interface between organism and environment.

Most research to date has focused on plant responses and adaptations to single features of the environment, but plants in nature often encounter multiple stresses. Effects of interacting environmental factors may be far from additive. For example, damage by high light, or photoinhibition, is dramatically increased when high-light exposure is accompanied by water stress or unusually low or high temperatures (Powles 1984). Physiological ecology, which combines techniques for assessing the environment, quantifying multiple components of plant responses, and integrating plant responses to the level of ecological success or agricultural yield, is well suited to the study of plant responses to multiple factors. Here, we examine resource interactions at levels of organization ranging from the cell to the ecosystem, focusing on carbon (as an index of the energy stored in organic

molecules) and nitrogen. We emphasize these resources because they often limit plant growth and because they illustrate the concepts necessary for extending the approach. Our primary tool is cost-benefit analysis, assessing the cost of acquiring one resource in terms of expending another and defining benefits in terms of effects on plant growth (Bloom et al. 1985).

Nutrient acquisition

Carbon cost of nitrogen acquisition. Nitrogen is the mineral nutrient that plants require in greatest quantity and that most frequently limits growth in both agricultural and natural systems. The carbon expended in acquiring nitrogen can make up a significant, if not predominant, fraction of the total energy a plant consumes. Plants have developed several approaches to nitrogen acquisition, including such diverse phenomena as fixation of atmospheric nitrogen, mycorrhizal associations, and carnivory. Yet most plants obtain their nitrogen entirely through root absorption of the inorganic ions ammonium and nitrate. The carbon costs for these various methods differ. We predict that the preferred method depends in large part on the carbon and nitrogen status of the plant and on the relative availability of energy and nitrogen in the environment.

Nitrogen acquisition consists of several processes: absorption, bringing nitrogen from the environment into the plant; translocation, moving inorganic nitrogen within the plant;

and assimilation, converting nitrogen from inorganic to organic forms.

ABSORPTION. Carbon costs for absorption may be subdivided between growth and maintenance of absorbing organs (generally roots) and the transport of minerals against a concentration gradient. For a wide variety of plants, roots account for 50–80% of annual dry matter production. The cost of producing a unit of root biomass is similar to that for other plant tissues (Lambers et al. 1983); thus, a large biomass allocation to roots represents a substantial carbon cost. This investment is necessary because soil deposits of mineral nitrogen, ammonium or nitrate, are usually so small that absorption quickly depletes the soil in immediate contact with the roots. Only through constant and extensive growth can roots mine a sufficient volume of soil to meet the nitrogen needs of a rapidly growing plant.

Unusual methods of nitrogen acquisition have additional carbon costs for growth and maintenance of absorbing organs. Nitrogen-fixing plants (those with bacterial symbionts that convert gaseous nitrogen into ammonium) incur the substantial expense of constructing root nodules and of providing bacterial symbionts with substrates for maintenance and growth (Minchin et al. 1981). Mycorrhizal fungi have small-diameter hyphae that increase the surface area of the root system but cost ten percent more to construct than the equivalent mass of roots (Harley and Smith 1983). Maintenance of mycorrhizas also consumes five to ten percent of the total plant carbon resources (Clarkson 1985). Carnivorous plants, which obtain mineral nutrients from animal prey, require expensive enticement and capture structures.

The carbon costs of ammonium and nitrate transport have not been clearly established. Absorption of these ions into the root appears to depend on active transport by specific carriers that are similar among different species (Bloom 1985). Calculations based on the energy requirement for ion transport into organelles or for moving nutrients against the concentration gradient from the soil solution to the root cytoplasm suggest that ion transport consumes an insignificant portion of root respiratory

energy (Clarkson 1985). Experimental verification of these calculations has been hampered by the lack of appropriate techniques. Recent developments permitting simultaneous measurement of root respiration and ammonium or nitrate absorption (Bloom and Epstein 1984) show that the costs of transport and absorption may be substantial, from 5–20% of the total plant respiration (Bloom unpublished data, Veen 1980).

TRANSLOCATION. The carbon cost of nitrogen translocation depends on the site of assimilation. Because ammonium is toxic at high concentrations in plant tissues, it is usually assimilated into organic forms near the site where it is absorbed or generated. Thus the cost of ammonium translocation to the assimilation site is negligible. Similarly, plants that assimilate nitrate in the roots should have negligible translocation costs. In contrast, species that assimilate nitrate in the leaves must bear significant translocation costs. Nitrate assimilation in leaves generates an ion imbalance, which is corrected by an organic acid shuttle that consumes roughly three percent of the total carbon budget (Raven and Smith 1976).

ASSIMILATION. The various methods of nitrogen assimilation differ greatly in carbon costs. Mycorrhizas transfer to the host nitrogen that is already in the form of amino acids (Harley and Smith 1983). Carnivorous plants catabolize the nitrogen of their prey to amino acids (Pate 1983). In contrast the conversion from ammonium to amino acid requires the transfer of 2 electrons and the catalysis of 1 ATP; nitrate assimilation requires 10 electrons and 1 ATP; nitrogen fixation requires 4–5 electrons and 7–10 ATP per nitrogen atom. Thus, the energy cost of nitrogen assimilation increases from mycorrhizas and carnivory to ammonium to nitrate to nitrogen fixation.

In species that assimilate nitrate in leaves, assimilation can be partially driven by photosynthetic electron transport. When light is not limiting to photosynthesis, nitrate assimilation in these species diverts relatively little energy away from photosynthetic carbon assimilation, and thus the carbon cost of nitrate assimilation is minor (McDermitt and Loomis

1981). However, in nonphotosynthetic tissue or when light limits photosynthesis, the cost of nitrate assimilation is substantial, diverting from carbon assimilation up to 15% of the total energy production (Bloom unpublished data, Penning de Vries et al. 1974). Ammonium assimilation in roots, which must be driven by respiratory energy, may expend two to five percent of net photosynthetic carbon gain (Oaks and Hirel 1985). Nitrogen fixation costs from 25–40% of total net photosynthetic carbon gain (Phillips 1980).

In summary, if root growth for nitrogen acquisition is about 10% of total plant production, the fraction of the carbon budget spent on nitrogen acquisition (absorption, translocation, and assimilation) ranges from 25–45% for ammonium, 20–50% for nitrate, 40–55% for nitrogen fixation, and 25–50% for mycorrhizas. These crude estimates support the contention that nitrogen acquisition is a major carbon expense.

Carbon constraints on nitrogen acquisition. The relative advantages of each nitrogen acquisition method shift with the availability of the different nitrogen forms and with the relative limitation of growth by carbon and nitrogen. Gaseous nitrogen is always abundant, but acquiring this form through nitrogen fixation entails the highest carbon cost. In environments where nitrogen limits growth more than does carbon, nitrogen fixation becomes advantageous. Early successional sites, for example, are often colonized by species that form nitrogen-fixing symbioses. As the availability of ammonium or nitrate increase and the availability of light decreases, nitrogen fixation becomes less prevalent (Pate 1983).

Preference for ammonium versus nitrate as a nitrogen source varies greatly among species. Some species, such as cranberry, can use only ammonium, whereas others, such as radish, are extremely intolerant of ammonium. Most species, however, grow best in a mixture of ammonium and nitrate, with the relative rates of ammonium and nitrate acquisition depending on the typical availabilities of these ions in the native habitat (Bloom 1985). Ambient light may also influence the choice between am-

monium and nitrate (Pate 1983): high light permits nitrate assimilation at little carbon cost and should thus favor the use of nitrate; conversely, the low respiratory costs of ammonium assimilation should favor acquisition of this form in low light.

Being able to use several different forms of nitrogen probably affords plants some of the flexibility needed to maintain an adequate carbon and nitrogen balance under fluctuating environmental conditions. Studies of these phenomena are relatively few because of such difficulties as the high mobility of soil nitrate, the rapid conversion of ammonium to nitrate and nitrate to nitrogen gas by soil microorganisms, and the need to measure in situ nitrate reduction or nitrogen fixation. Slowly metabolized, radioactive analogues of ammonium and nitrate (methylamine and chlorate, respectively), more extensive use of the stable isotope ^{15}N , and measurement of the assimilatory quotient (ratio of CO_2 consumed to O_2 evolved, Bloom 1985) could provide an effective approach to these problems.

Photosynthesis

Photosynthesis-nitrogen relationship.

We can consider the nitrogen costs of carbon gain with an approach parallel to that for assessing the carbon costs of acquiring nitrogen. The parallel is not exact, because, unlike carbon compounds, nitrogen compounds are not oxidized as energy substrates. They are, however, committed to biological functions: nitrogen invested in one process is not simultaneously available for use in another. The nitrogen investment required to yield a given carbon gain is an index of the nitrogen cost of carbon acquisition. Though many aspects of plant form and function influence carbon gain and require nitrogen, we will limit our discussion to photosynthesis because its nitrogen costs are currently the subject of intensive research.

Approximately 75% of the nitrogen in a plant leaf with C_3 photosynthesis, the pathway used by most of the world's plants, is invested in chloroplasts, and most of that is invested in photosynthesis (Figure 1). Since nitrogen frequently limits growth and since most leaf nitrogen is invested in components of photosynthesis, understanding the nitrogen-photosynthesis relationship is likely to be critical for several issues in ecology and

agriculture. For example, if nitrogen controls photosynthesis, then the ability to acquire nitrogen may be a primary determinant of above-ground growth. Alternatively, manipulating the nitrogen-photosynthesis relationship may provide effective routes toward increasing agricultural production without increasing nitrogen fertilization.

Photosynthetic capacity, i.e., the maximum rate of carbon assimilation by a single leaf at light saturation and optimal conditions, is highly correlated with leaf organic nitrogen content (Figure 2). This close correlation is observed when the variation in leaf nitrogen results from differences among species (Mooney et al. 1981), leaf age (Field and Mooney 1983), nitrogen availability during growth (Evans 1983), or light levels during growth (Gulmon and Chu 1981). The generality of the nitrogen-photosynthesis relationship strongly suggests that one or several nitrogenous leaf components directly limit photosynthetic capacity. To date, the strongest evidence for direct limitation by a single nitrogenous component comes from studies of ribulose-1,5-bisphosphate carboxylase-oxygenase (RUBISCO), the primary CO_2 -fixing en-

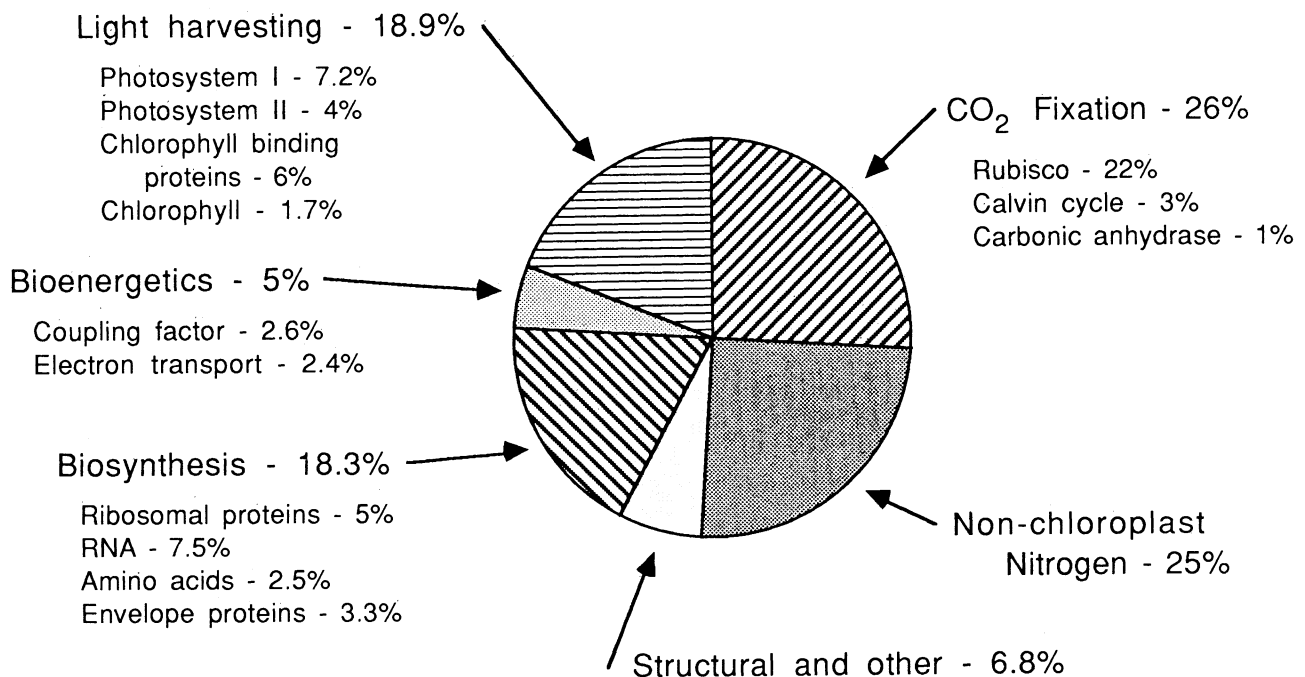


Figure 1. The proportional allocation of leaf nitrogen in a sun leaf of a plant with C_3 photosynthesis. The photosynthetic compartments are those labeled light harvesting, CO_2 fixation, and bioenergetics. Data from Evans (1983 and unpublished); figure courtesy of J. R. Seemann, Desert Research Institute, Reno, NV.

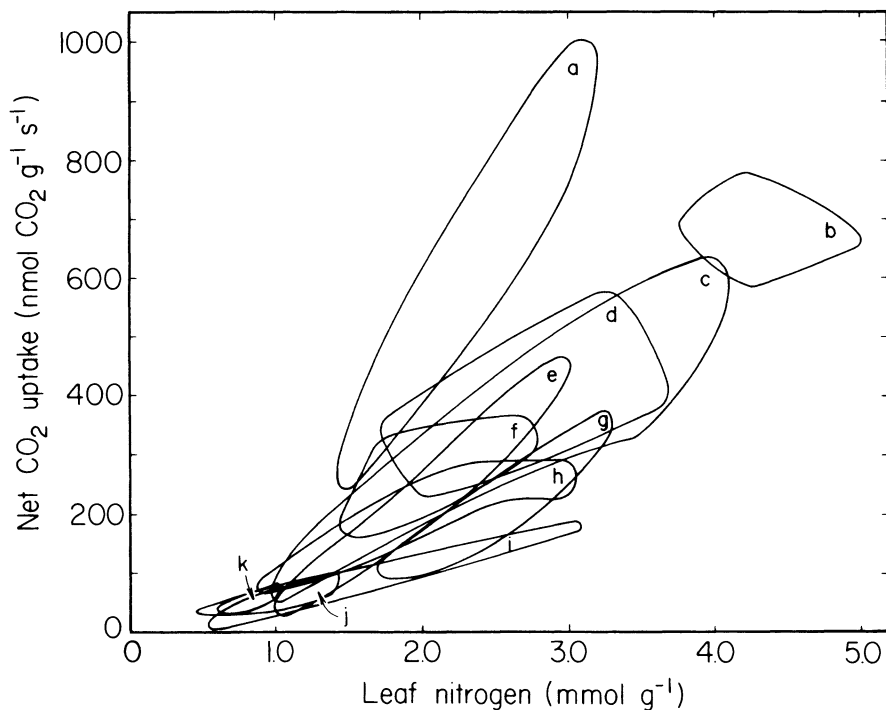


Figure 2. The relationship between photosynthesis and nitrogen for a wide variety of plant species. Each outline circumscribes all the data reported in a single study. Included are data from 33 C_3 species (b through k) and 11 C_4 species (a). Some of the data are from naturally grown plants, and some are from plants grown in controlled environments. The experimental variables manipulated to introduce variation in photosynthetic capacity and nitrogen include nitrogen availability, light availability, and leaf age. Adapted from Field and Mooney (1986).

zyme in C_3 plants and the ultimate CO_2 -fixing enzyme in plants with the C_4 and CAM photosynthetic pathways (Caemmerer and Farquhar 1981). The importance of such limitation, however, should vary with light and CO_2 availability and with the partitioning of nitrogen among potentially limiting factors. In comparison to sun plants (as shown in Figure 1), shade plants invest much less nitrogen in RUBISCO and more in light harvesting, compensating for the scarcity of light relative to CO_2 in shady habitats (Björkman 1981).

Mechanisms controlling the abundance as well as the activity of limiting components are attuned to the environment at many levels of organization. For example, at the level of gene expression, levels of messenger RNA for the (nuclear-coded) small subunit of RUBISCO are controlled by light (Kaufman et al. 1984). Catalytic activation of RUBISCO is modulated by CO_2 , magnesium, and light (Seemann et al. 1985). In individual leaves, RUBISCO level is controlled by nitrogen availability during

growth (Evans 1983), as well as by levels of CO_2 , light, and water stress (Caemmerer and Farquhar 1984). At the whole plant level, partial defoliation increases RUBISCO in remaining leaves (Caemmerer and Farquhar 1984). At the community level, interspecific differences in the catalytic properties of RUBISCO may be important components of ecological differentiation. Although RUBISCO is clearly important in limiting photosynthesis, it is probably not the only rate-limiting nitrogenous compound. Environmental controls on other limiting components of photosynthesis are less well understood, but they are probably coordinated with controls on RUBISCO.

Efficiency of nitrogen use. A plant allocates nitrogen most efficiently when nitrogen is equally limiting to each plant process (Bloom et al. 1985). Thus, efficiency of nitrogen investment in photosynthesis is maximized when two conditions are met: each of the nitrogenous components of photosynthesis must be equally

limiting; and investment of nitrogen in photosynthesis should never exceed the level at which some alternative investment, for example in other leaves, roots, or reproductive structures, yields greater returns. A useful starting point in evaluating the efficiency of nitrogen investment in photosynthesis is to consider the ratio of photosynthetic capacity to leaf nitrogen, an index of potential photosynthesis under optimal conditions. We term this ratio potential photosynthetic nitrogen use efficiency (PPNUE).

In leaves with low nitrogen content PPNUE is low and it increases with increasing nitrogen (Figure 3). Above nitrogen levels of about 1.7 mmol/g (2.4%), a trend is not obvious for the broad comparison in Figure 3, but some data indicate that within a species, PPNUE decreases with increasing nitrogen beyond a critical level (Evans 1983). Leaves with low nitrogen probably have low PPNUE because they invest a large proportion of the total leaf nitrogen in nonphotosynthetic components, such as the nucleic acids and proteins associated with cell regulation and respiration. Decreases in PPNUE at high nitrogen may result from allocating nitrogen to storage forms or from an increased limit to photosynthesis by nonnitrogenous components.

PPNUE is a measure of the instantaneous efficiency of using nitrogen to fix carbon. Leaves with low nitrogen contents are often long lived. When net carbon gain is summed over the total life of the leaf, low-nitrogen, long-lived leaves may achieve the same or a greater lifetime carbon gain than high-nitrogen, short-lived leaves (Small 1972). Low-nitrogen contents may be favored in long-lived leaves because low-nitrogen leaves are relatively insensitive to nitrogen loss via leaching (Tukey 1970) and are relatively unattractive to herbivores. Further, if leaves persist for an extended time, they may encounter conditions under which high nitrogen yields either little or no benefit in photosynthesis. This final possibility—that high leaf nitrogen is not always an advantage—is particularly relevant for plants confronted with other resource limitations, among which light and water limitations are especially important.

Light-nitrogen interactions. Leaf nitrogen is closely correlated with photosynthetic capacity when photosynthesis is measured at light saturation. But at low light, photosynthesis increases little, if at all, with increasing leaf nitrogen (Gulmon and Chu 1981). Because high-nitrogen leaves have high maintenance requirements, they typically have higher dark respiration than low-nitrogen leaves and therefore lose more carbon in darkness. Thus, for leaves in low-light habitats, increasing leaf nitrogen above low levels yields small gains in photosynthesis. From this we can predict low nitrogen in leaves of shade-adapted plants, a prediction generally supported by numerous studies. The low nitrogen in leaves of shade plants is especially dramatic when expressed on the basis of leaf area because many shade plants decrease nitrogen and construction costs in parallel by manufacturing thin leaves (Björkman 1981). Within a single plant, leaves near the top of the canopy often experience high light while leaves near the bottom are continuously shaded. This intracanopy environmental variability makes the distribution of nitrogen among leaves an important determinant of whole-canopy photosynthesis. For a given investment in nitrogen, whole-canopy photosynthesis is maximized when leaves near the top of the canopy are high in nitrogen, and leaves near the bottom are low in nitrogen (Field 1983). We predict that the importance of an efficient nitrogen distribution increases with the magnitude of the intracanopy habitat variation.

Water-nitrogen interactions. In C_3 plants, photosynthesis is generally limited by both the biochemical potential to fix CO_2 and the rate of CO_2 diffusion through stomata. Because stomata serve as a pathway for both CO_2 diffusion into and water diffusion out of the leaf, plants cannot decrease the diffusional limitation to photosynthesis by increasing stomatal conductance without simultaneously increasing water loss. This coupling between CO_2 and water exchange imposes broad constraints on patterns of nitrogen investment and water use. When limited water availability forces plants to operate at low stomatal conductances (thereby de-

creasing water use), increasing leaf nitrogen produces diminishing returns in photosynthesis and leads to a dominant limitation of photosynthesis by stomata (Mooney and Gulmon 1979). Under these conditions, investment of nitrogen in photosynthesis is likely to yield benefits greater than costs only at low leaf-nitrogen levels. The low nitrogen contents in leaves of desert and chaparral evergreens support this interpretation, but because arid habitats are often low in nitrogen availability, a more quantitative analysis is needed.

Although water availability imposes broad constraints on nitrogen investment, subtle variations in water and nitrogen use may be important components of ecological differentiation among co-occurring species. Partial stomatal closure increases photosynthesis per unit of water loss but decreases total photosynthesis, and therefore photosynthesis per unit of nitrogen. An increase in leaf nitrogen without an increase in conductance increases photosynthesis, and photosynthesis per unit of water loss, but tends to decrease photosynthesis per unit of nitrogen because stomatal limitation increases. Thus, a given habitat may support equally successful plants with a range of water use patterns, if this range is balanced by

differences in nitrogen investment (Field et al. 1983).

Until recently, interpretations of water use in relation to carbon gain have been based on short-term measurements of photosynthesis and transpiration. But an exciting discovery has led to a technique now being increasingly applied to ecophysiological studies. The discovery was that the extent to which leaves discriminate against CO_2 containing the naturally occurring isotope ^{13}C varies with the physiological status of the leaf in a manner than can be related to the balance between photosynthesis and transpiration (Farquhar et al. 1982). Because CO_2 is, through photosynthesis, incorporated into plant structure, plant tissues form an integrated record of carbon isotope discrimination and hence of the relationship between photosynthesis and transpiration. This technique, along with recent advances in the instrumentation for measuring gas exchange by plants, dramatically increases the potential resolution and breadth of ecophysiological studies focused on carbon-nutrient-water interactions.

Allocation and growth

Allocation. One of the major mechanisms by which plants adjust to re-

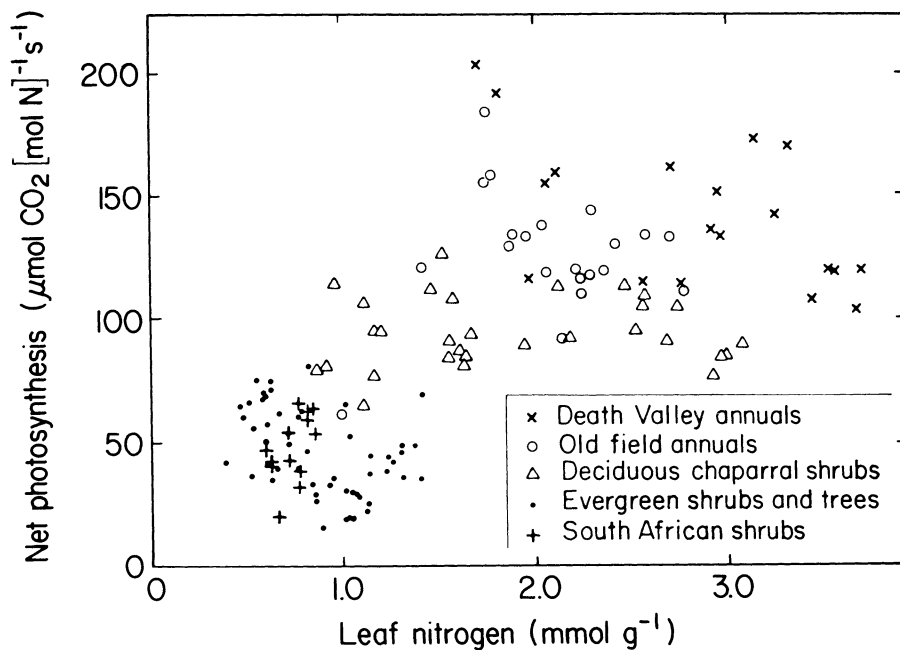


Figure 3. Potential photosynthetic nitrogen use efficiency (PPNUE), or photosynthetic capacity per unit of leaf nitrogen, as a function of leaf nitrogen for 21 species of naturally growing C_3 plants representing a wide variety of growth forms and habitats. Adapted from Field and Mooney (1986).

source imbalance is by allocating new biomass to the organs that acquire the most strongly limiting resources. For example, when plants become short of carbon (e.g., by shading or herbivores that remove photosynthetic tissue) or have a relative surplus of nitrogen, they compensate by producing proportionately more shoot and less root material (Chapin 1980). The resulting decrease in root:shoot ratio reduces carbon stress and returns carbon and nutrient reserves to a balance more favorable for growth. Conversely, when nutrient limitations lead to low nutrient concentrations and to accumulation of carbohydrates, plants respond by increasing their energy allocation to root growth, leading to a more favorable carbon:nutrient balance.

Plants also compensate for specific nutrient imbalances. For example, nitrogen-deficient plants exhibit a high capacity to absorb ammonium and nitrate; potassium-deficient plants have a high potential to absorb potassium (Glass 1983). Plant roots are also more prone to mycorrhizal colonization as nutrient availability declines. This further increases the absorptive potential of the root system, although at a substantial carbon cost.

Growth. With all other factors equal, natural selection probably favors a high growth rate, close to the maximum that can be maintained in any given environment. Plants characteristic of resource-rich environments tend to have high potential growth rates, and plants characteristic of resource-poor environments tend to have low potential growth rates (Grime 1977). The abundance of plants with low potential growth rates seems paradoxical, unless one considers the factors that make high potential growth rates yield low realized growth in low-resource environments. Possible factors include a trade-off between a high relative growth rate and efficiency of resource use or the capacity to accumulate reserves during rare periods of high resource supply, so that these reserves can continue to support growth during later periods of low supply (Chapin 1980).

Resource loss and resource use efficiency. Plants respond to a low-re-

source environment by reducing the rate of tissue loss. Individuals within a species tend to increase leaf and root longevity in response to nutrient stress, and in an ecosystem the proportion of evergreen species increases as habitat fertility decreases (Shaver 1983). By reducing resource loss, plants of low-resource habitats reduce their resource demand and are better able to achieve an internal balance favorable for growth. Conservation through decreased loss can be specific to those resources that most strongly limit growth. For example, nutrient-stressed plants lose less nutrients by leaching (Tukey 1970) and generally translocate a larger proportion of nutrients from senescing leaves (retranslocation) before abscission than do plants growing on more fertile soils (Shaver and Melillo 1984). These factors contribute to the high nutrient-use efficiency of plants growing on infertile soils (Vitousek 1982). There is, however, little evidence that species native to infertile soils are more efficient in retranslocation or nutrient use than species native to fertile sites when both types of species are grown under the same conditions (Chapin and Kedrowski 1983).

In response to drought, plants typically reduce transpiration rates by partial stomatal closure; this reduces the water loss more than the photosynthetic carbon gain, increasing water use efficiency (i.e., carbon gain per unit water loss). Similarly, shade plants have low rates of dark respiration and photorespiration, characteristics that reduce carbon loss under carbon stress so that they use photosynthetically gained carbon more efficiently (Björkman 1981).

In summary, plants respond to resource limitation with growth and allocation responses that tend to increase the efficiency with which they use the limiting resources. Especially important are reduction of tissue loss and conservation of the resources that most strongly limit growth.

Single or multiple limiting factors?

Plants possess substantial homeostatic capabilities that reduce imbalances among the environmental resources required for growth. Such compensation is seldom complete, however, because the environment is constantly

changing, so a plant cannot achieve perfect equilibrium with its resource base, and because certain habitats, such as deserts, present extreme resource imbalances. If plants have not entirely compensated for resource imbalance, Liebig's law of the minimum should apply. This hypothesis states that plant growth is limited by a single resource at any one time; only after that resource is increased to the point of sufficiency can another resource enhance plant growth. However, if plants compensate perfectly for resource imbalance in the environment, growth should be equally limited by all resources (Bloom et al. 1985).

Field experiments using natural plant communities frequently indicate that two or more resources simultaneously limit plant growth. For example, growth of several species in arid grasslands responds to either nitrogen or water (Lauenroth et al. 1978). In Alaskan tundra, plant growth responds to temperature, light, and nutrients (Chapin and Shaver 1985). These results suggest that either plants in these communities are simultaneously limited by several environmental resources or limitation switches among different resources so quickly during the growing season that, over the time scale of the measurements, it is not possible to identify a single limiting factor. In either case, plants are clearly successful in compensating for resource imbalance, even in extreme environments.

The compensatory response to multiple resource limitations is also evident from growth chamber experiments. *Impatiens parviflora*, a forest understory herb, responds to additions of light, nitrogen, or phosphorus when grown under conditions simulating its natural habitat (Peace and Grubb 1982). Such simultaneous limitation by multiple resources has at least three potential advantages. First, multiple limitation indicates efficient investment in resource acquisition. Limitation by a single resource implies excess capacity for acquiring nonlimiting resources. This excess could potentially be redirected toward acquiring the limiting resource or toward other aspects of growth and reproduction. Second, plants simultaneously limited by several resources can benefit from various re-

source additions to the environment. Third, as is evident from the study of Peace and Grubb (1982), plants limited by multiple resources respond synergistically to the addition of multiple resources, i.e., the growth response to added fertilizer plus light was much greater than if the responses had been simply additive. Similar synergistic responses to the addition of more than one nutrient or nutrient plus water are common in field experiments (Chapin and Shaver 1985, Lauenroth et al. 1978).

Ecosystem implications

Natural plant communities are normally composed of several species, each with slightly different physiological characteristics and requirements. Consequently, each species in a community may be limited by a slightly different combination of resources. For example, when light, nutrients, and temperature were altered in two tundra communities, each species showed a different pattern of response (Chapin and Shaver 1985). Similarly, each species responds differently to annual variations in environment. Years that are favorable for growth of some species reduce the growth of other species, both because of direct plant responses and competitive interactions. Consequently, community productivity is much more stable in the face of environmental variation than is the productivity of any individual species (Chapin and Shaver 1985). Interspecific variation in resource requirements almost certainly plays a role in community population dynamics comparable in importance to its role in community productivity. Collaborations between physiological ecologists and ecosystem and community ecologists will be a key to developing a mechanistic understanding of the dynamics of complex natural communities.

Herbivory and resource levels. The carbon:nitrogen balance of a plant determines not only its own pattern of resource acquisition and use but also its susceptibility to herbivores and pathogens and, therefore, the trophic dynamics of the ecosystem. Through evolution plants have developed diverse morphological and chemical defenses against herbivores

and pathogens. Defense is a costly proposition. Morphological defenses entail construction costs. Chemical defenses require metabolic expenditures, which may be great if concentrations of defensive compounds are high or if they are rapidly recycled (Mooney and Gulmon 1982).

In general, defense allocations increase with environmental stress (Bryant et al. 1983). Species characteristic of stressful environments have reduced potentials for growth, even under favorable conditions, and the tissues that they produce are long-lived. High levels of defense in these tissues presumably increase the probability that they persist through all or much of their potential lifespans.

Within species, a given genotype can vary the quantity of defensive metabolites in response to herbivory (Haukioja 1980) or changes in resource availability (Bryant et al. 1983, Waring et al. 1985). When conditions are favorable, plants allocate resources preferentially to growth rather than defense, so levels of secondary metabolites tend to decline. When a specific resource (e.g., nitrogen) limits growth, however, the plant tends to accumulate other resources (e.g., carbon) and uses these to increase synthesis of secondary

metabolites (Bryant et al. 1983). For example, tropical forests on nitrogen-poor soils are evergreen and produce leaves rich in lignin and tannin, two major carbon-based secondary compounds. Herbivory in these forests is very low, often restricted to fruits and seeds (Garlan et al. 1980). In contrast, plants grown under low light but with an abundance of nutrients produce leaves with low concentrations of carbon-based defensive substances (phenolics, tannins, lignin) and high concentrations of soluble nitrogen. These plants are selectively attacked by defoliating insects (Table 1).

The possibility that host susceptibility can be altered by modifying growing conditions has important management implications. Game managers interested in producing palatable foliage may strive to alter the relative availability of critical resources to increase the nutritional value of foliage while still maintaining a growth rate sufficient to assure perpetuation of the vegetation. Alternatively, foresters may seek a different balance of resources that maximizes defense and minimizes palatability. In a 120-year lodgepole pine forest, for example, treatments leading to a high carbon:nutrient balance also conferred a high resistance against bark

Table 1. Chemical composition of willow leaves (*Salix dasyclados*) under specified environments permitting constant relative growth rates (Waring et al. 1985), and consumption by leaf beetles (*Galerucella lineola*) given free access for 26 hours (Larsson et al. 1986).

	High light High nutrients	Low light High nutrients	High light Moderate nutrients
Chemical Component			
Phenolics (relative units)	100 ^a	30 ^b	76 ^a
Tanins (relative units)	65 ^a	64 ^a	100 ^b
Leaf nitrogen (mg N/dm ²)	21.5 ^a	13.5 ^b	14.0 ^b
Amino acids (mg N/dm ²)	2.4 ^a	2.3 ^a	0.9 ^b
Nitrate (mg N/dm ²)	1.0 ^a	1.7 ^b	0.0 ^c
Starch (% dry weight)	5.1 ^a	5.3 ^a	20.7 ^b
Lignin (% dry weight)	20.8 ^a	13.4 ^b	24.5 ^c
Consumption by beetles (mg/plant)	0.18 ^a	1.00 ^b	0.20 ^{ab}

Within each row, values with different superscripts differ significantly at $P < 0.05$.

beetles (Waring and Pitman 1985). Introduction of nitrogen-fixing species into communities where carbohydrate reserves already limit plant growth could further reduce carbon-rich defensive compounds and increase the amount of herbivory. Similarly, the impact of air pollution or acid rain rich in nitrogen and sulfur should be studied in light of the effects on carbon:nutrient balance and the expected increase in the susceptibility of forests to insect pests and pathogens (Nihlgard 1985).

Future research directions

Past research in physiological ecology has focused on plant adaptation to single environmental stresses. However, most natural environments are stressful with respect to more than one resource, and the nature of these stresses changes with time and location. Relatively little work has been done in the area of plant responses to multiple environmental stresses. We suggest that future research should emphasize two areas: mechanistic studies of the responses of individual plants to multiple environmental stresses and studies of the responses of species mixtures to variation in environment. The first approach will provide insight into modes of plant response; the second addresses community- and ecosystem-level problems with ecophysiological approaches.

At the individual plant level, we need a more quantitative accounting of the costs and benefits of the various responses to changes in resource balance. We have shown that the carbon cost of nitrogen acquisition is large and varies with the source of nitrogen and with light availability. Similarly, patterns of nitrogen investment and carbon gain per unit of nitrogen vary with the environment. These relationships require more careful quantification, evaluation in a wider range of systems, and further mechanistic exploration to identify targets for possible manipulation. Further, they must be related to overall plant performance, as measured by growth and reproduction.

A second major goal at the individual plant level should be to explore the physiological, biochemical, morphological, and phenological adaptations of plants to specific resource

imbalances. The shade-tolerant herb *Impatiens parviflora* responds to nutrient addition at all levels of light intensity, whereas shade-intolerant species respond to nutrients only under high light (Peace and Grubb 1982). Species clearly differ in their potential to compensate for resource imbalance, yet little is known about adaptations to specific resource imbalances.

Another important area warranting increased research activity is the interface between ecophysiology and community ecology. Research here provides a context for interpreting the results of ecophysiology, and it identifies and quantifies mechanisms through which species interact in nature. Little research has been done in this area, and the greatest initial success is expected from studies of relatively simple communities, either artificial ones in the laboratory (Austin and Austin 1980) or natural ones with relatively few species. Studies of community responses to biotic as well as abiotic environmental factors are also needed.

Conclusions

Plants exhibit an impressive potential to compensate for imbalances in the availability of environmental resources. Generally, resources are allocated most efficiently when growth is equally limited by all resources. In the case of carbon and nitrogen, because the carbon costs of nitrogen acquisition and the nitrogen costs of carbon acquisition are high, plants adjust the expenditure of internal reserves to acquire these resources from the environment in approximately constant proportions. If either resource is scarce, reserves of the other are expended in acquiring the first so that both carbon and nitrogen become effectively limiting. Plants also increase the efficiency of resource use in such environments by restricting the rate of resource loss. An understanding of resource balance in plants requires further examination of plant-environment interactions and promises to yield useful insights for managing the trophic dynamics of natural ecosystems.

Acknowledgments

This is Carnegie Institution of Wash-

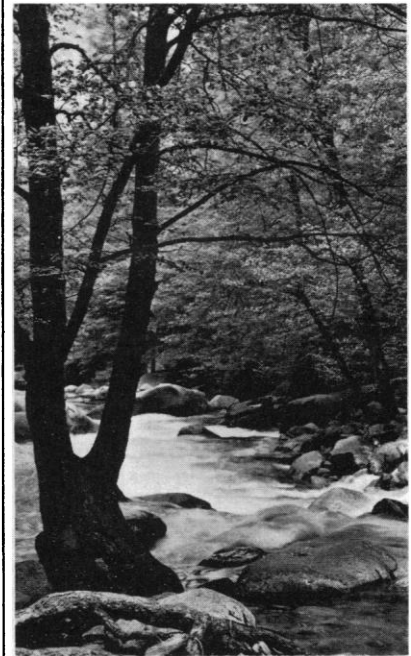
ington, Department of Plant Biology, Publication number 915.

References cited

- Austin, M. P., and B. O. Austin. 1980. Behavior of experimental plant communities along a nutrient gradient. *J. Ecol.* 68: 891-918.
- Björkman, O. 1981. Responses to different quantum flux densities. Pages 57-107 in O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, eds. *Physiological Plant Ecology. I. Responses to the Physical Environment*. Springer-Verlag, Berlin, FRG.
- Bloom, A. J. 1985. Wild and cultivated barleys show similar affinities for mineral nitrogen. *Oecologia* 65: 555-557.
- Bloom, A. J., F. S. Chapin III, and H. A. Mooney. 1985. Resource limitation in plants—an economic analogy. *Annu. Rev. Ecol. Syst.* 16: 363-392.
- Bloom, A. J., and E. Epstein. 1984. Varietal differences in salt induced respiration in barley. *Plant Sci. Lett.* 35: 1-3.
- Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357-368.
- Caemmerer, S., and G. D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* 153: 376-387.
- . 1984. Effects of partial defoliation, changes of irradiance during growth, short term water stress and growth at enhanced p(CO₂) on the photosynthetic capacity of leaves of *Phaseolus vulgaris* L. *Planta* 160: 320-329.
- Chapin, F. S., III. 1980. The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11: 233-260.
- Chapin, F. S., III, and R. A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* 64: 376-391.
- Chapin, F. S., III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* 66: 564-576.
- Clarkson, D. T. 1985. Factors affecting mineral nutrient acquisition by plants. *Annu. Rev. Plant Physiol.* 36: 77-115.
- Dowling, P., F. S. Chapin III, F. E. Wielgolaski, and P. Kilfeather. 1981. Nutrients in tundra ecosystems. Pages 647-683 in L. C. Bliss, O. W. Heal, and J. J. More, eds. *Tundra Ecosystems: A Comparative Analysis*. Cambridge University Press, Cambridge, UK.
- Evans, J. R. 1983. Nitrogen and photosynthesis in the flag leaf of wheat (*Triticum aestivum* L.) *Plant Physiol.* 72: 297-302.
- Farquhar, G. D., M. H. O'Leary, and J. A. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Aust. J. Plant Physiol.* 9: 121-137.
- Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program. *Oecologia* 56: 341-347.
- Field, C., J. Merino, and H. A. Mooney. 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. *Oecologia* 60: 384-389.

- Field, C., and H. A. Mooney. 1983. Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. *Oecologia* 56: 348-355.
- . 1986. The photosynthesis-nitrogen relationship in wild plants. Pages 25-55 in T. J. Givnish, ed. *On the Economy of Plant Form and Function*. Cambridge University Press, Cambridge, UK.
- Gartlan, J. S., D. B. McKey, P. G. Waterman, C. N. Mbi, and T. T. Struhsaker. 1980. A comparative study of the phytochemistry of two African rain forests. *Biochem. Syst. Ecol.* 8: 401-422.
- Glass, A. D. M. 1983. Regulation of ion transport. *Annu. Rev. Plant Physiol.* 34: 311-326.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111: 1169-1174.
- Gulmon, S. L., and C. C. Chu. 1981. The effects of light and nitrogen on photosynthesis, leaf characteristics, and dry matter allocation in the chaparral shrub, *Diplacus aurantiacus*. *Oecologia* 49: 207-212.
- Harley, J. L., and S. E. Smith. 1983. *Mycorrhizal Symbiosis*. Academic Press, London.
- Haukioja, E. 1980. On the role of plant defenses in the fluctuation of herbivore populations. *Oikos* 35: 202-213.
- Kaufman, L. S., W. S. Thompson, and W. R. Briggs. 1984. Different red light requirements for phytochrome-induced accumulation of *cab* RNA and *rbcS* RNA. *Science* 226: 1447-1449.
- Lambers, H., R. K. Szaniawski, and R. De Visser. 1983. Respiration for growth, maintenance and ion uptake. An evaluation of concepts, methods, values, and their significance. *Physiol. Plant.* 58: 556-563.
- Larsson, S., A. Wiren, L. Lundgren, and T. Ericsson. 1986. Effects of light and nutrient stress on leaf phenolic chemistry in *Salix dasyclados* and susceptibility to *Galerucella lineola* (COL. CHRYSOMELIDAE). *Oikos*, in press.
- Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* 36: 211-222.
- McDermitt, D. K., and R. S. Loomis. 1981. Elemental composition of biomass and its relation to energy content, growth efficiency and growth yield. *Ann. Bot.* 48: 275-290.
- Minchin, F. R., R. J. Summerfield, P. Hedley, E. H. Roberts, and S. Rawthorne. 1981. Carbon and nitrogen nutrition of nodulated roots of grain legumes. *Plant Cell Environ.* 4: 5-26.
- Mooney, H. A., C. Field, S. L. Gulmon, and F. A. Bazzaz. 1981. Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. *Oecologia* 50: 109-112.
- Mooney, H. A., and S. L. Gulmon. 1979. Environmental and evolutionary constraints on the photosynthetic characteristics of higher plants. Pages 316-337 in O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven, eds. *Topics in Plant Population Biology*. Columbia University Press, New York.
- . 1982. Constraints on leaf structure and function in reference to herbivory. *BioScience* 32: 198-206.
- Nihlgard, B. 1985. The ammonium hypothesis—an additional explanation to forest dieback in Europe. *Ambio* 14: 2-8.
- Oaks, A., and B. Hirel. 1985. Nitrogen metabolism in roots. *Annu. Rev. Plant Physiol.* 36: 345-365.
- Pate, J. S. 1983. Patterns of nitrogen metabolism in higher plants and their ecological significance. Pages 225-255 in J. A. Lee, S. McNeill, and I. H. Rorison, eds. *Nitrogen as an Ecological Factor*. Blackwell Scientific Publ., Oxford, UK.
- Peace, W. J. H., and P. J. Grubb. 1982. Interaction of light and mineral nutrient supply in the growth of *Impatiens parviflora*. *New Phytol.* 90: 127-150.
- Penning de Vries, F. W. T., A. H. M. Brunsting, and H. H. Van Laar. 1974. Products, requirements, and efficiency of biosynthesis: a quantitative approach. *J. Theor. Biol.* 45: 339-377.
- Phillips, D. A. 1980. Efficiency of symbiotic nitrogen fixation in legumes. *Annu. Rev. Plant Physiol.* 31: 29-49.
- Powles, S. 1984. Photoinhibition of photosynthesis induced by visible light. *Annu. Rev. Plant Physiol.* 35: 15-44.
- Raven, J. A., and F. A. Smith. 1976. Nitrogen assimilation and transport in vascular land plants in relation to intracellular pH regulation. *New Phytol.* 76: 415-431.
- Seemann, J. R., J. A. Berry, S. M. Freas, and M. A. Krump. 1985. Regulation of ribulose biphosphate carboxylase activity in vivo by a light modulated inhibitor of catalysis. *Proc. Nat. Acad. Sci.* 82: 8024-8028.
- Shaver, G. R. 1983. Mineral nutrition and leaf longevity in *Ledum palustre*: the role of individual nutrients and the timing of leaf mortality. *Oecologia* 56: 160-165.
- Shaver, G. R., and J. M. Melillo. 1984. Nutrient budgets of marsh plants: efficiency concepts and relation to availability. *Ecology* 65: 1491-1510.
- Small, E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Can. J. Bot.* 50: 2227-2233.
- Tukey, H. B., Jr. 1970. The leaching of substances from plants. *Annu. Rev. Plant Physiol.* 21: 305-324.
- Veen, B. W. 1980. Energy costs of ion transport. Pages 187-195 in G. W. Rains, R. C. Valentine, and A. Hollaender, eds. *Genetic Engineering of Osmoregulation: Impact on Plant Production for Food, Chemicals, and Energy*. Plenum Press, New York.
- . 1982. Nutrient cycling and nutrient use efficiency. *Am. Nat.* 119: 553-572.
- Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285-298.
- Waring, R. H., A. J. S. McDonald, S. Laarson, T. Ericsson, A. Wiren, E. Arwidsson, A. Ericsson, and T. Lohammer. 1985. Differences in chemical composition of plants grown at constant relative growth rates with stable mineral nutrition. *Oecologia* 66: 157-160.
- Waring, R. H., and G. B. Pitman. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66: 889-897.

To Explore, Enjoy, and Protect



Bruce Barnbaum

You and I share a great love of this earth.

The ocean's pounding surf, Spring covering the earth with that season's newness, a bird's song reaching out . . . and we are moved.

Our curiosity calls us. We explore a bit. Some travel to a distant wilderness, some no farther than a corner of the back yard. But each of us looks and listens to the wonder of the natural world around us.

We enjoy the earth's beauty, it's grandeur. The endless sweep of colors, and sounds, and everywhere, the excitement of life.

But there are some that do not see the wonder of it all. And so we, of the Sierra Club, join together to protect the earth.

We work for legislation that guarantees clean air and water. To regulate the use and disposal of poisonous toxic chemicals. To set aside the most special places for parks and wilderness.

We invite you to join with us.

To explore, to enjoy. To protect this wondrous earth. For all of us . . . forever.

For membership information, write Sierra Club, 530 Bush Street, San Francisco, CA 94108, (415) 981-8634.



**Sierra
Club**