Resource Limitation in Plants--An Economic Analogy

Arnold J. Bloom; F. Stuart Chapin, III; Harold A. Mooney


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RESOURCE LIMITATION IN PLANTS—AN ECONOMIC ANALOGY

Arnold J. Bloom
Department of Vegetable Crops, University of California, Davis, California 95616

F. Stuart Chapin, III
Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99701

Harold A. Mooney
Department of Biological Sciences, Stanford University, Stanford, California 94305

INTRODUCTION

The fields of economics and ecology share more than terminology: economic models have proven valuable for describing diverse aspects of animal behavior (28, 107, 119); ecological concepts have aided the study of economic systems in primitive human societies (16); and both economic and ecological considerations have influenced policy on natural resource utilization (5). Plant ecologists, despite allusions to resource budgets (27, 90), cost-benefit analyses (50, 105), and marginal rates of return (92, 93), have yet to evaluate fully the applicability of economic theory to plant processes. Here we place the relationship between plant growth and resource balance in an economic perspective. We have chosen to focus on general principles, rather than to attempt an exhaustive literature review of resource limitations in plants. The economic theory outlined below is discussed in most introductory textbooks on microeconomics (e.g. 80).

A plant has many parallels with a business firm. From the environment a plant must acquire resources (water, nutrients, carbon, etc) that it can then save (storage) or spend in various ways to construct a product (leaves, stems, roots, etc). This product can then assist in the acquisition of additional resources. In
addition, both plants and businesses must operate under changing conditions. A highly successful strategy in one climate may prove disastrous in another: Optimal solutions are usually ephemeral. Thus, plants and businesses must engage in long-term as well as short-term planning.

A major complication in extrapolating from economics to ecology, however, is that money, a central construct in economic theory, has no simple analogue in biological systems. Most cost-benefit analyses of vegetative processes have considered carbon as the sole currency (19, 90, 93, 105). Yet plants utilize several types of resources (carbon, nutrients, and water) that they gain, save, and spend. Water or nutrients may be more relevant measures in environments where the availability of these resources most strongly limits production. In lacking a common currency, plants are similar to primitive human societies that operate on a barter system for the exchange of goods or services. Anthropologists as well as plant ecologists need to focus on the factors governing the exchange rate among resources under different circumstances.

A second potential source of confusion lies in the distinction between external and internal resources. Resource acquisition entails the absorption of a resource into the plant, translocation within the plant, and assimilation into the form that will be stored or immediately utilized. Once a resource is acquired, it becomes part of the internal reserves. Plants must then expend some of these internal reserves of resources to acquire additional external resources. Table 1 defines the major terms used in this review and gives their economic and ecological interpretations.

Several characteristics of higher plants facilitate the evaluation of economic parameters: (a) The critical resources for plants fall naturally into just three categories—carbon, nutrients, and water; (b) most plants require these resources in similar proportions to sustain rapid growth (41, 47, 62), and thus the demand for resources is relatively uniform; (c) responses of plants to changes in the availability of a single resource generally can be monitored under realistic conditions; (d) individuals that are identical genetically can be produced through vegetative propagation to provide replicated measurements (variation in natural populations does, however, present a constraint on simple interpretation); (e) plants interact in a competitive manner with minimal sociological behavior, thus approximating the condition of perfect competition required by many economic analyses; and (f) technological change in plant processes, such as the evolution of C₄ photosynthesis, occurs slowly so as to simplify investment decisions. Consequently, the simplifying assumptions that economists make to render their mathematical approach tractable may be more reasonable for plant systems than for human systems; many of the successful applications of economic theory pertain to crop production, e.g. the optimal allocation of fertilizer in the production of corn (59).
<table>
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<tr>
<th>Term</th>
<th>Economic definition</th>
<th>Ecological definition</th>
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<tr>
<td>Process</td>
<td>Necessary business function, e.g. manufacturing or marketing</td>
<td>Necessary biological function, e.g. growth, maintenance, or defense</td>
</tr>
<tr>
<td>Resource</td>
<td>Raw materials required for a process, e.g. steel or labor (g or h)</td>
<td>Materials in the environment or within the plant required for a process (g of C, N, or H₂O)</td>
</tr>
<tr>
<td>Reserve</td>
<td>Internally stored resource (g)</td>
<td>Internally stored resource (g of C, N, or H₂O)</td>
</tr>
<tr>
<td>Product Supply</td>
<td>Good or service (g or hr)</td>
<td>Biomass (g of C, N, or H₂O)</td>
</tr>
<tr>
<td>Availability of a resource at the site of a process (g/hr or h/hr)</td>
<td>Availability of a resource at the site of a process (g/h of C, N, or H₂O)</td>
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<tr>
<td>Demand</td>
<td>Requirement for a resource at the site of a process (g/hr or hr/hr)</td>
<td>Requirement for a resource at the site of a process (g/h of C, N, or H₂O)</td>
</tr>
<tr>
<td>Cost</td>
<td>Money spent per unit resource ($/g or $/hr)</td>
<td>Reserves expended to increase the supply of a resource (e.g. g C expended/g N acquired)</td>
</tr>
<tr>
<td>Revenue</td>
<td>Gross income ($)</td>
<td>Gross resource gain (g of C, N, or H₂O)</td>
</tr>
<tr>
<td>Profit</td>
<td>Revenue minus cost ($)</td>
<td>Net resource gain (g of C, N, or H₂O)</td>
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<tr>
<td>Marginal Product</td>
<td>Change in production per change in resource supply (dg product/dg resource)</td>
<td>Growth response to change in resource supply (dg biomass/dg of C, N, or H₂O)</td>
</tr>
<tr>
<td>Exchange Ratio</td>
<td>Relative cost of two resources ($/$)</td>
<td>Relative quantities of two resources acquired per expenditure of reserve (e.g. g C/g N per expenditure of g H₂O)</td>
</tr>
<tr>
<td>Marginal Rate of Technical Substitution</td>
<td>Increase in supply of one resource necessary to compensate for loss of another and still maintain the same production level (dg/dg, dhr/dg, or dhr/dhr)</td>
<td>Increase in supply of one resource necessary to compensate for loss of another and still maintain the same growth rate (e.g. dg C/dg N)</td>
</tr>
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</table>

**ECONOMIC THEORY**

Economists generally assume that every business firm seeks to maximize its profits and that only profitable firms survive. Similarly, ecologists assume that natural selection tends to maximize the fitness of an individual. In this review, we assume that the fitness of a plant—its genetic contribution to future generations—is a function of its primary productivity, because both the quantity and quality of reproductive output is highly correlated with primary productivity.
(57, 137). The relationship is particularly strong between vegetative reproduction and primary productivity (57). We recognize that other components of fitness, such as age of first reproduction, show no clear correlation with productivity (137). These issues are also amenable to economic analysis (risk and decision analysis), but are beyond the scope of the present review. We now present four economic theorems on profit maximization and optimal resource allocation and discuss their significance to plant productivity.

**Theorem 1**

A profit-maximizing firm buys resources at the lowest price and uses them when they are most valuable. The cost of a resource may be fixed or variable, depending on the extent to which the cost fluctuates during a relatively short time or over a longer time according to production level. Costs, when variable, reflect supply and demand; for example, a scarce resource that is needed immediately will have a high cost.

Most plant resources have variable costs because their supply fluctuates through the growing season. Plants can maximize their primary productivity (profits) by “buying” low and by making timely “reinvestment,” i.e. by acquiring a resource when it is abundant, storing it, and utilizing it when it provides maximum enhancement of productivity. In a following section, we consider the cost and benefit of storage.

**Theorem 2**

A profit-maximizing firm seeks the output level for which marginal cost equals marginal revenue. Marginal cost and marginal revenue are the change in cost or revenue, respectively, resulting from a change in production. For both business firms and plants, marginal cost normally decreases, attains a minimum, and then increases as production level rises. The initial decrease results from economies of scale: Producing a second toaster or leaf may not require facilities beyond those used to produce the first toaster or leaf. However, when production exceeds a certain level, not only do existing facilities become inadequate, but coordination among the various components of production becomes less efficient. For example, the production of many new leaves may require development of new supporting structures or vascular tissue. This phenomenon (known in economic parlance as the law of diminishing marginal returns) leads to higher marginal costs as the production level rises. Marginal revenue, on the other hand, steadily declines as the production level rises: The price a business can charge for a toaster decreases as the availability of toasters increases; self-shading limits the relative gain in photosynthetic capacity attained through leaf production.

Because the relationship between marginal cost and marginal revenue changes with the production level, a firm should increase production as long as
the increment in cost per unit produced is less than the increment in revenue. By analogy, net photosynthesis (carbon profit) equals the difference between gross photosynthesis (revenue) and respiration (cost). To maximize net photosynthesis, a plant continues to produce new leaves until the increment in gross photosynthesis equals the increment in respiration.

**Theorem 3**

A profit-maximizing firm tends to equalize the ratio of marginal product over cost for all resources. The marginal product of a resource is the change in production resulting from a change in resource input. By this theorem, a firm should continue to buy a given resource as long as the corresponding increase in production is greater than could be achieved by the same expenditure for any other resource. The ratio of marginal product over cost represents the ratio of benefit to cost for a resource; profits are maximized when the ratio of benefit to cost is the same for all resources.

In biological terms the marginal product of a resource is simply the response of primary productivity to a change in availability of carbon, nutrients, or water (i.e. the slope of the response curve). By this theorem, a plant should adjust allocation so that, for a given expenditure in acquiring each resource, it achieves the same growth response: Growth is equally limited by all resources.

**Theorem 4**

Internal resources are optimally allocated among competing processes when each resource limits all processes to the same degree. Most firms carry out several processes (e.g. manufacturing, packaging, marketing) and have different internal resources (e.g. labor, capital) that they can expend for each process. To some extent these resources are interchangeable (e.g. if more capital is used in manufacturing, less labor may be required to achieve the same level of output). The firm must decide how much of each resource to expend for each process. The marginal rate of technical substitution (MRTS) of a process is the change in quantity of one resource required to substitute for another in order to maintain the same production level; the MRTS is equal to the ratio of the marginal products for the two resources \( \text{MRTS}_{ij} = \frac{MP_i}{MP_j} \). If a firm has limited resources, optimal allocation of resources among processes conducted by the firm necessitates that the MRTS be the same for all processes (e.g. substituting labor for capital should have the same effect upon manufacturing and packaging).

Internal plant resources, or reserves, can also substitute for one another. For example, carbon substitutes for nitrogen in the use of phenolics instead of alkaloids as protection against herbivory (95) or in the use of sugars instead of amino acids as osmoticants (118). By this theorem, optimal allocation within the plant is achieved when a given balance of reserves is equally limiting to each
plant process. Therefore, an increment in some limiting reserve should stimulate each plant process to the same degree.

In summary, economic theory predicts the following about plant processes:

Prediction 1. Storage enables plants to acquire resources at minimal cost and to use them at times of maximal benefit.

Prediction 2. Plants continue to produce leaves or roots until the marginal revenue from this increased production is equal to the marginal cost.

Prediction 3. Plants adjust allocation so that their growth is equally limited by all resources.

Prediction 4. Each plant process is limited by the same balance of internal reserves.

In the economy of plants, as in other barter systems, the relative costs of resources (i.e. exchange ratios) can be more informative parameters than are absolute costs. For example, the extent to which a given resource is limiting (Theorems 3 and 4) depends upon its exchange ratio with other resources, not its absolute cost. The above theory suggests:

Prediction 5. In order to achieve both a similar benefit-to-cost ratio for each resource (Theorem 3) and an optimal allocation among processes (Theorem 4), plants adjust physiologically in both the short-term (acclimation) and the long-term (genetic adaptation) to minimize differences in exchange ratios across diverse habitats.

RESOURCE ACQUISITION

The economic theory discussed above implicates the exchange ratio—defined as the relative amount of two resources that can be acquired for a given expenditure of reserve—as a key parameter for predicting plant responses to changes in the balance among external and internal resources. Previous studies of optimal allocation and resource acquisition have focused on the expenditure of a single reserve for the acquisition of a single resource, e.g. carbon acquisition as a function of water loss (33) or nitrogen content (43). Exchange ratios, which should provide a broader perspective, have not been characterized. In the following, we discuss resource acquisition in terms of exchange ratios and outline the sensitivity of these ratios to environmental variation.

The exchange ratio between two resources depends on (a) their supply, (b) the demand for them, and (c) the type of reserve being expended. As the supply of one resource (e.g. carbon) decreases with respect to another (e.g. water), the exchange ratio between them \((C_c/C_w)\) increases. Similarly, if the demand for a limited resource (e.g. carbon) increases, its exchange ratios with other re-
sources (e.g. water and nutrients) will increase \((C_c/C_w\) and \(C_c/C_n\) increase). To acquire a resource generally requires a different amount of each reserve (e.g. carbon assimilation requires different expenditures of nutrient and water reserves); consequently, the exchange ratio varies with the type of reserve being expended \((C_c/C_w\) in terms of nitrogen may differ from \(C_c/C_w\) in terms of phosphorus). In the following sections, we examine the influence of environment on supply and demand and, in turn, the effects of these factors and the type of expenditure on exchange ratios. We then consider the extent to which plants adjust physiologically in order to equalize exchange ratios across diverse habitats (Prediction 5). The information on nutrients emphasizes nitrogen and phosphorus, the two nutrients whose availability most frequently limits primary productivity.

**Carbon and Nutrients**

The relative supplies of carbon and nutrients differ greatly among habitats. For example, the carbon-to-nutrient balance may be very low in the forest understory \((55, 110)\) and may be very high in the tundra or desert \((4, 27, 52, 157)\). This variation in supply results in strong habitat differences in the exchange ratio between carbon and nutrients.

Within a given environment, however, supplies of carbon and nutrients often change synchronously in the short- and long-term. In the short-term, the spring flush of growth common to seasonal environments results both from a pulse of nutrient availability as the soil thaws or as the rains return \((127, 144)\) and from the high photon flux density (PFD), i.e. the carbon supply, of an open canopy. On the other hand, rainy weather may increase nutrient supply through improved soil-water status (cf section on Water and Nutrients, below) but decrease carbon supply through reduced PFD. In the longer term, both nutrient and carbon supplies increase after a fire or tree fall due to more rapid nutrient release from organic matter and greater light penetration \((26, 125, 141, 151)\). In summary, for a given habitat, the relative supply of carbon and nutrients may remain fairly constant.

The relative demand for carbon and nutrients in the production of tissue is reflected in the nutrient content of that tissue, i.e. nutrient-to-carbon ratio. Even under uniform growth conditions, this ratio differs substantially among \((a)\) species—200% \((21; \) C. Field, H. A. Mooney, unpublished information), \((b)\) genotypes of a species—50% \((128)\), \((c)\) tissues of a single plant—300% \((128)\), and \((d)\) development stage of a given tissue—50% \((21, 44, 76)\). This variation in demand for carbon and nutrients should be reflected in a variable exchange ratio, \(C_c/C_n\).

The relative cost of carbon and nutrient acquisition, i.e. the exchange ratio between carbon and nutrients, depends on the internal resource being expended.
1. In terms of water, carbon acquisition usually has higher cost than nutrient acquisition as a result of the high transpiration rates associated with photosynthesis. Under sudden drought, this exchange ratio becomes more extreme, because water stress inhibits carbon acquisition to a greater extent than nutrient acquisition; consequently, nutrient content tends to increase with drought (56).

2. Likewise, the nutrient cost of carbon acquisition is higher than that of nutrient acquisition. This assertion is based on observations that (a) nutrient concentrations (particularly, nitrogen) are greater in leaves than in roots (21, 41, 128) and (b) carbon acquisition is directly proportional to leaf nitrogen levels (43, 103), whereas the influx of a particular nutrient is inversely related to root concentrations of that nutrient (51, 58, 78).

3. The carbon cost is generally less for carbon acquisition than for nutrient acquisition, because the rate of maintenance respiration is much higher for roots than shoots (1, 72) and because the energy required for assimilation is at least twice as great per unit NO$_3^-$ or SO$_4^{2-}$ than per unit CO$_2$ (64, 115).

In summary, the water and nutrient costs of carbon acquisition are usually greater than those of nutrient acquisition, whereas the carbon cost of carbon acquisition is usually less than that of nutrient acquisition; thus, the exchange ratio between carbon and nutrients, $C_c/C_n$, will be greater in terms of water and nutrients than in terms of carbon.

These considerations—variation in relative supply and demand and differential costs of resource acquisition—indicate that the exchange ratio between carbon and nutrients is highly variable, both seasonally and across different habitats.

Plants reduce disparity in supplies of carbon and nutrients by increasing their capacity to acquire the most limiting resource. Processes that determine a plant’s capacity for carbon and nutrient acquisition often compete with one another for internal reserves. For example, reserves allocated to root growth or symbiotic microorganisms enhance nutrient absorption at the immediate expense of shoot growth and carbon assimilation; in addition, direct coupling of nitrogen or sulfur reduction to photosynthetic electron transport may deprive carbon fixation of energy (102, 155). By increasing shoot growth in low-light environments at the expense of root growth, a plant robs its capacity for nutrient acquisition to pay for a greater capacity for carbon acquisition (cf section on Growth, below) but equalizes carbon and nutrient supplies.

Plants can moderate relative demands for carbon and nutrients through prudent use of stored resources and flexible growth requirements (cf sections on Storage and on Growth, below). In infertile soils, plants accumulate high concentrations of carbon-rich compounds such as carbohydrate, resin, and lignin but have low nutrient contents (18, 27, 90, 158), whereas in low-light
environments, plants accumulate high nutrient concentrations but have low carbohydrate contents (10, 11, 83). Thus, plants change their demands for carbon and nutrients in response to a skewed supply.

Compensatory shifts in both relative acquisition capacities (supplies) and relative demands of production reduce variation in the exchange ratio between carbon and nutrient. Prediction 5—plants adjust physiologically to minimize changes in exchange ratios—seems consistent with this general trend.

Water and Nutrients

Water supply in the soil strongly influences nutrient supply. As water becomes more limited, (a) decreased soil water movement reduces mass flow of nutrients to the roots; (b) shrinkage of both soil particles and roots reduces contact between them and, consequently, reduces nutrient diffusion; (c) increased concentration in the soil solution of exchangeable cations like calcium reduces the activity of anions such as phosphate because of the low solubility of salts like calcium phosphate; and (d) decreased mineralization reduces the rate of nutrient replenishment into the soil solution (104). Moreover, seasonal environments often experience simultaneous pulses of high water and nutrient availability: During the spring, snowmelt increases water availability concurrently with the release of nutrients from the soil as a result of freeze-thaw processes and elevated temperatures (127, 144). Because water and nutrient supplies vary concomitantly in a given environment, the effect of supply on the exchange ratio between water and nutrients is minimal.

Demands for water and nutrients may be similar. Ontological changes in leaf water and nutrient contents generally occur in parallel so that the apparent tissue concentrations of nutrients are relatively constant (74). Fluxes of water and nutrients into developing fruits and seeds are highly correlated (109). Water movement through the plant can, in special cases, determine nutrient movement. For example, the unusually high transpiration rate observed in the mistletoes appears necessary for these parasites to obtain sufficient nitrogen from the xylem of the host (40, 132). In addition, the distribution of calcium in plants is determined to a large extent by water movement (67). Consequently, in some circumstances, the relative demands for water and nutrients remain constant; thus, the effect of demand on their exchange ratio is also minimal.

Nonetheless, under most circumstances, the demands for water and for nutrients vary independently. Large fluctuations in transpiration have little influence on either nutrient absorption (130) or flux of nitrate through the xylem (134) indicating that the demand for water need not affect the demand for nutrients. Similarly, the demand for nutrients need not affect that for water; water use efficiency does not significantly change with nutrient deprivation (145). Herbivory, or clipping of shoots to simulate herbivory, reduces trans-
piration, but in some species, it increases the capacity of the remaining roots for nutrient absorption (82; but see 35).

The exchange ratio between water and nutrients is not sensitive to the type of reserve being expended because the capacities for water and nutrient acquisition are closely aligned. The root is the major organ for both processes. Root hairs are highly active in the uptake of water as well as nutrients (104). Under water- or nutrient-limited conditions, mycorrhizae associations serve to enhance the acquisition of both resources (101). Overall, expenditure of any resource to enhance water acquisition generally serves to enhance nutrient acquisition and vice versa.

The exchange ratio between water and nutrients, \( C_w/C_n \), should be relatively uniform in a given environment because the factors of supply and demand are highly interdependent and the type of reserve expenditure is unimportant. This exchange ratio, however, may vary from a low value for bogs (79) to a high one for many agricultural systems (120). Plants from habitats where the availabilities of water and nutrients are greatly imbalanced exhibit physiological adaptations that tend to equalize the exchange ratio. On one extreme, carnivorous pitcher plants from bogs literally capture nutrients in exposed pools of water (60, 77); on the other extreme, *Nolana mollis*, a succulent shrub from the coastal desert of Chile, secretes hydrosopic salts on its leaves to capture water (94). More commonly, plants under water or salinity stress employ both inorganic ions (e.g. potassium, sodium, or nitrate) and nitrogen-rich organic compounds (e.g. glycinebetaine and proline) to maintain a positive water balance (56, 100, 160). In all these cases, greater expenditure of an abundant reserve enhances the capacity to acquire a scarce resource. This serves to moderate the exchange ratio between water and nutrients across habitats and seems to support Prediction 5.

**Carbon and Water**

Supplies of carbon and water are often inversely related. Precipitation supplements the water supply, but reduces the photon flux density (PFD), i.e. carbon supply. Conversely, conditions associated with high PFD typically increase evaporation and transpiration, thereby decreasing water availability in the soil. This inverse pattern of carbon and water supplies contributes to a highly variable exchange ratio between these resources in natural ecosystems.

In contrast, the demands for carbon and water are correlated. Stomatal aperture concomitantly controls CO\(_2\) diffusion into and water loss out of a leaf so that high carbon demand entails high water demand. Growth and, consequently, carbon demand are reduced under water stress by stomatal limitations to carbon assimilation and by lack of adequate turgor for cell expansion (61). Therefore, the relative amounts of carbon and water in plant tissues do not vary greatly; tissue water content seldom decreases more than 20% even under
severe water stress (122); in comparison, tissue nutrient contents are often halved under nutrient deficiencies (128).

The relative costs of acquiring carbon and water, i.e., the exchange ratio, vary greatly with the resource being expended.

1. The water cost of carbon acquisition predominantly results from the water loss through the stomata during CO₂ assimilation (131). This loss can be very high [between 50 and 1000 g H₂O lost per g CO₂ acquired (90)] because for water, in comparison to CO₂, the concentration gradient between the plant and atmosphere is steeper, the diffusion rate through the stomata is faster, and the resistance pathway from the atmosphere to the plant is shorter. In contrast, the water cost of carbon acquisition is relatively low, requiring only sufficient water to maintain viable root tissue. Thus, the water cost of carbon acquisition is greater than that of water acquisition.

2. The relative nutrient costs of carbon and water acquisition depend on water availability. When water is not limiting, carbon acquisition has higher nutrient costs than water acquisition, because leaves have higher nutrient requirements than roots (cf section on Carbon and Nutrients, above). However, under water or salinity stress, plants may accumulate high levels of nutrient-rich osmoticants to maintain a positive water balance (cf Water and Nutrients); a concentration of 100 meq provides only about 0.5 MPa of osmotic pressure. Consequently, the nutrient cost of water acquisition may exceed that of carbon acquisition under conditions of extreme drought.

3. The relative carbon costs of carbon and water acquisition may be more constant than the relative water or nutrient costs. If the carbon cost of root growth and maintenance is deducted, the respiratory efficiency of roots is similar to that of shoots (1, 72). In addition, water stress can increase the carbon cost of both carbon and water acquisition: The carbon cost of CO₂ assimilation increases through higher mesophyll resistance and lower quantum yields (111); the carbon cost of water acquisition increases through more rapid root death (42, 70) and with the requirement for osmoticants such as sugars, organic acids, and polyols (100, 118, 160).

In summary, the exchange ratio between carbon and water, $C_c/C_w$, is higher in terms of water reserves than in terms of carbon reserves. This exchange ratio in terms of nutrient reserves is variable with degree of water stress.

The above considerations—the inverse relationship between carbon and water supplies, the proportional relationship between demands, and variable acquisition costs—suggest that the exchange ratio between carbon and water varies greatly both seasonally and among habitats. Several plant adaptations tend to moderate this exchange ratio. In deserts, which are high-carbon but low-water environments, plants with C₄ or Crassulacean Acid metabolism
trade a higher carbon cost of carbon acquisition for a lower water cost. These pathways have a higher carbon cost because they require carboxylation of phosphoenolpyruvate in addition to the carboxylation of ribulose-1,5-bisphosphate. C₄ plants have a lower water cost because they can sustain carbon assimilation at lower internal CO₂ concentrations. Crassulacean Acid Metabolism plants have a lower water cost because they can acquire carbon at night when humidity is higher (106). Another example from the desert is provided by succulents with rapid root growth that trade a higher carbon cost of water acquisition for a higher water acquisition capacity. In the understory of a tropical rain forest, which is a low-carbon but high-water environment, stomata close slowly in the absence of light so as to permit better utilization of sunflecks (112), thus trading a higher water cost of carbon acquisition for a lower carbon cost.

**Summary of Exchange Ratios**

The exchange ratios among carbon, nutrients, and water generally exhibit spatial variation (habitat), but need not—particularly between water and nutrients—exhibit temporal variation (seasonal or successional). To avoid extreme exchange ratios, plants seem to balance supply and demand (Prediction 5). They adjust supply by increasing allocation of internal reserves to the acquisition of scarce resources and adjust demands by varying storage and growth patterns. The following sections discuss in detail the influence of storage and growth on the economy of a plant.

**STORAGE**

In the following we assess the economics of storage, noting why dissimilar growth forms may differ in their storage patterns.

**Economics of Storage**

Investment in growth results in a compounding of the investment in terms of new resources gained. A diversion of these new resources to storage, rather than growth, results in a loss of the compound interest (indirect costs). In addition, there are direct costs associated with storage that include movement of storage compounds to and from the site of storage (the carbon costs of phloem loading have been estimated as 10% of the amount of carbon translocated; 114), as well as costs of chemical conversion to specific storage compounds, and the costs of constructing any special cell or organelle in which the stores may be housed. Finally there may be direct costs associated with the protection of these compounds. Storage compounds, by their very nature, are resource-rich and provide prime targets for herbivores and pathogens. In a plant that seeks to maximize fitness, compensation for these direct and indirect costs should be
either (a) higher productivity at some future time when multiple resources are likely to be in more optimal balance than at present, or (b) survival of the individual after catastrophic events.

Not all of the resources necessary for plant growth may be available at the same time. Storage can act as a buffer between asynchrony of resource supply and the demand for resource use in growth. For example, in the Arctic in early spring the soil is frozen so that nutrients to support new growth of the tussock graminoid *Eriophorum vaginatum* must come from reserves rather than from the soil. In contrast, carbohydrate is supplied to new growth directly from photosynthate that is not environmentally limited at this time (23). Resource acquisition in excess of resource use for current growth is generally termed luxury consumption, a misnomer that results from considering only a fraction of the annual resource acquisition and allocation pattern of an individual. Resources such as nitrate (48) and phosphorus (31) have been shown to accumulate (store) in plants during periods of external abundance and to be consumed in subsequent growth when these resources are externally limited.

Resources may be stored by plants as insurance against catastrophe: to promote regrowth following fire, herbivory, drought, unusually cold temperatures, etc. These catastrophes may occur at infrequent and unpredictable intervals. Since immediate productivity will be reduced through storage (29, 92), the loss in competitive advantage from short-term resource accumulation must be balanced by long-term persistence in a variable environment (142). The amount of reserves necessary for reconstruction after tissue destruction no doubt is a function of the rapidity of canopy or root reconstruction. This probably is the reason that, in cold or arid environments, storage amounts are high (23). Also, in a sense, the annual unfavorable period—be it drought or cold temperature—that characterizes all but tropical wet climates, is a catastrophe and an event for which most perennial plants put aside stores to utilize in subsequent regrowth (97).

There is a period in the life cycle of most plants, namely seed germination, when the plant is totally cut off from the possibility of acquiring resources. Thus all resources necessary to build a new autotrophic individual must be constructed from reserves. The reserves contained in seeds are under constraints that may not operate in the above cases. First, the tissue in which reserves are stored in seeds is generally at a very low water potential. Secondly, with seeds there are generally size and weight constraints due to selection for dispersability. This results in an even greater premium on high-energy or resource-rich molecules than is the case for reserves held within the body of a mature plant.

In addition to the different storage requirements of dispersing units and rooted individuals, there are different limitations in the storage possibilities among various plant growth forms. Annuals, herbaceous perennials, and woody perennials may each have differing reserve patterns, as may evergreen
versus deciduous woody perennials. These patterns are related to both the economics of the direct costs of storage (conversion into resource-compounds, compartmentation, etc) and the indirect costs (loss of revenue through immediate growth) resulting from storage timing and duration. The particular storage pattern within a growth form will depend on the particular seasonal pattern of resource availability within its habitat; we discussed this below.

**Nature of Storage and Transport Compounds**

In general nitrogen-rich molecules such as amides (asparagine, 21.2% N, glutamine, 19.2% N) are the transport form of nitrogen (66). In fruit trees of the Rosaceae, arginine, which has a low C/N ratio (32.2% N), is the major storage form of nitrogen, along with glutamine and asparagine. Transport forms are aspartic acid, asparagine, and glutamine (146). In citrus, proline serves as a principal nitrogen storage molecule even though it is not a particularly nitrogen-rich molecule (12% N), perhaps because other aspects (osmoticum) of this molecule enable it to serve a multifunctional role (99).

Apparently most of the phosphorus in the xylem (7) as well as the phloem (162) moves in the inorganic form. During the growing season temporary accumulation of phosphorus is stored in an inorganic form in the vacuole (6, 7). However in the dormant season storage of phosphorus can take place in a large variety of organic compounds (phopholipids, P esters, nucleic acids, etc) that play multiple roles in the plant (22, 23).

Nonreducing sugars and sugar alcohols are the principal transport forms of carbon in higher plants. The preponderance of such transport substances is thought to be due to their solubility in water and their economy of construction from the first products of photosynthesis or from compounds readily produced in the breakdown of reserves. Species differ, however, in the principal sugar types utilized for transport, with some having predominantly either sucrose, oligosaccharides, or sugar alcohols. These transport compounds often differ from the storage compounds found in the same plant (162).

Starch and sucrose are the principal storage carbohydrates in plants although other polysaccharides such as mannans, xyloglucans, galactans, and fructans can also be important, particularly in composites and temperate grasses (84, 158). Nonstarch reserves are generally osmotically active and hence may play a role in frost-hardiness as well as serving other functions. Furthermore they can be mobilized faster than starch, which may explain why starch is found principally in tropical grasses while other polysaccharides are found in temperate grasses where rapid regrowth during the spring is at a premium (158). In vegetative tissues, polysaccharides are stored in the vacuole whereas in seeds these compounds are in the cell walls (84).

In summary, plants use storage compounds that can serve multiple roles, a practice that tends to reduce the direct costs of storage.
Protection of Stores

Storage compounds represent high concentrations of resources that are valuable for herbivore as well as plant growth. By their very nature, stores generally reside in nongrowing or slowly growing tissue. Stores can be protected from herbivores by location within the plant (e.g. belowground stores of graminoids) or by incorporation into toxic compounds. Relatively little is known about this latter possibility. Seeds of certain tropical plants contain toxic amino acids (e.g. canavanine, 30% N) that are degraded during germination (133). In leaves, alkaloids that have high nitrogen content, such as caffeine (29% N) and nicotine (17% N), have been noted to turn over and even to be translocated (95). Such an approach, however, does not appear common for the protection of carbohydrate reserves; for example, sugars linked into toxic glycosides probably are not reused (3).

Growth Form and Growth Stage Constraints

In evaluating the economics of storage, the constraints of growth form must be considered. These constraints relate to both direct and indirect costs: direct costs because growth form will determine the potential location for storage compounds; indirect costs (i.e. the loss of compound interest from immediate growth) because growth form influences the synchrony of resource acquisition.

There is a basic dichotomy in the storage forms for nutrients that occur in seeds as opposed to the vegetative body. In the mesophyll cells of hydrated tissues, vacuoles can serve to isolate osmotically active substances. Vacuoles are generally lacking in seeds, so that high concentrations of soluble compounds cannot be isolated from and, thus, potentially interfere with cytoplasmic function. For example, many deciduous trees store nitrogen in their seeds as protein and in their mature tissues as other soluble compounds (146, 152). In bark of apple and several taiga forest trees, however, nitrogen is predominantly stored in the form of proteins although at considerably lower concentrations than it occurs in seeds (e.g. approximately 3.5% protein per gram dry weight versus the 20–40% protein that occurs in seeds; 22, 65). Inorganic phosphorus, contained in cellular vacuoles, can be the principal storage compound in the vegetative body, whereas phytic acid serves the same role in seeds (6, 7).

Perennials generally have greater requirement and capacity for storing resources than do annuals. However, even annuals utilize stores of carbohydrate (29, 36), expending these stores late in their growth cycle when external resources are limited or when photosynthetic capacity becomes restricted by environment or extensive herbivory. There is also great variation in storage patterns even within co-occurring species of a single growth form. For example, among annuals—generally, small early flowering species—growth and uptake are directly linked and thus these plants maintain no nitrogen stores, (29,
108). Other annuals—usually, those with fleshy stems and leaves—store nitrate. Finally, there are annuals that store organic nitrogen (108).

The leaves of evergreen plants generally serve as storage organs for both carbon (96) and nutrients (21, 99). In a comparison of co-occurring deciduous and evergreen trees Chapin & Kedrowski (23) noted no difference in the kinds of storage compounds present but only in their location. The storage of resources in evergreen leaves obviates the need for and the associated carbon costs of winter translocation of reserves to other plant parts.

Control of Storage Resource Use

Controls over storage utilization have not been adequately studied. Apparently not all reserves are depleted in any given growth cycle—rather, some short-term reserves are kept for long-term use, a point we discuss below. How is such control effected? Moreover, plants may experience more than one period of reserve depletion between periods of new resource acquisition. For example, stored carbohydrate supports fruit production after leaf fall on the tree *Aesculus californica*, but sufficient reserves remain several months later to build a new canopy (96). How is such a division of reserve pools accomplished?

GROWTH

Growth is a measure of the net resource gain from the environment and, in that it is related to fitness (cf section on Economic Theory), is analogous to the profit of a business firm. For plants, as for firms, it is crucial to decide whether to reinvest new growth or profit into either (a) increased capacity for resource acquisition, (b) storage, or (c) the creation of new subsidiaries. The choice of increased capacity has the direct potential for compounding the investment by enhancing growth rate. Economic theory suggests how and to what extent plants should increase their capacity for resource acquisition in order to maximize growth in a particular environment.

The Extent of Growth

Plants continue to produce leaves or roots until the marginal revenue equals the marginal cost (Prediction 2). Simulation models built upon this assumption often provide a realistic representation of controls over plant growth. For example, canopy growth models often assume that leaf growth continues until a leaf area index (LAI) is achieved that maximizes canopy photosynthesis (88, 93). This assumption has been verified in crop species, where the maximum observed LAI generally coincides with maximum canopy photosynthesis (89). The biological mechanism of equalizing marginal cost and marginal revenue (with respect to the carbon balance of a leaf) involves developmental changes in the flux of carbohydrates through the phloem; developing leaves support their
growth in part by the importation of carbohydrate from the phloem, whereas mature leaves cannot normally acquire carbohydrates from the rest of the plant (98). Consequently, a leaf senesces when it experiences a negative carbon balance. Less information is available for roots, but by this theorem, we predict that a plant ceases to produce roots in those soil zones where the nutrient or water return is less than the investment of these resources in new roots. Clearly, fine root proliferation is considerably reduced in zones of low nutrient availability (37–39) and root growth declines as the soil dries (42, 69, 70).

**Growth Costs**

The carbon cost to produce a unit of tissue can be calculated from the chemical composition of that tissue multiplied by the biosynthetic cost of each component (85, 86, 88, 90, 114), or it can be predicted from the gross chemical composition of the tissue (81). Synthesis of certain constituents such as lipids, resins, or lignins requires two- to three-fold more energy than synthesis of polysaccharides (Table 2).

Although plant species and parts often differ by a factor of 2 or 3 in concentration of individual constituents, there is generally only a 20–30% range in carbon cost of synthesis (Table 3), because the total amount of

<table>
<thead>
<tr>
<th>Component</th>
<th>Concentration (% dry weight)</th>
<th>Cost of synthesis (mg g⁻¹ product)</th>
<th>Retranslocation (% of initial pool)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>C</td>
<td>N</td>
</tr>
<tr>
<td>Cellulose</td>
<td>21.2</td>
<td>470</td>
<td>0</td>
</tr>
<tr>
<td>Hemicellulose</td>
<td>30.9</td>
<td>470</td>
<td>0</td>
</tr>
<tr>
<td>Lignin</td>
<td>3.9</td>
<td>860</td>
<td>0</td>
</tr>
<tr>
<td>Condensed tannin</td>
<td>1.9</td>
<td>770</td>
<td>0</td>
</tr>
<tr>
<td>Hydrolyzable tannin</td>
<td>2.9</td>
<td>770</td>
<td>0</td>
</tr>
<tr>
<td>Polysaccharide</td>
<td>11.9</td>
<td>450</td>
<td>0</td>
</tr>
<tr>
<td>Sugar</td>
<td>9.0</td>
<td>440</td>
<td>0</td>
</tr>
<tr>
<td>Lipid</td>
<td>3.6</td>
<td>1210</td>
<td>0</td>
</tr>
<tr>
<td>Protein</td>
<td>10.0</td>
<td>650</td>
<td>121</td>
</tr>
<tr>
<td>Amino acid</td>
<td>0.7</td>
<td>650</td>
<td>121</td>
</tr>
<tr>
<td>Nucleic acid</td>
<td>1.0</td>
<td>650</td>
<td>155</td>
</tr>
<tr>
<td>Chlorophyll/lipoprotein</td>
<td>0.9</td>
<td>1210</td>
<td>63</td>
</tr>
<tr>
<td>Phospholipid</td>
<td>0.8</td>
<td>1210</td>
<td>0</td>
</tr>
<tr>
<td>Sugar phosphate</td>
<td>0.3</td>
<td>440</td>
<td>0</td>
</tr>
<tr>
<td>Minerals</td>
<td>1.1</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Total cost</td>
<td></td>
<td>550</td>
<td>15.1</td>
</tr>
</tbody>
</table>

*Table 2* The concentration of various organic constituents in leaves of a tundra sedge (*Eriophorum vaginatum*); the carbon, nitrogen, and phosphorus cost of synthesis of each constituent; and the proportion of each constituent that is retranslocated in autumn. [Data is from Chapin et al (23)].
Table 3  Nitrogen and carbon costs of synthesis for leaves of plants from different ecosystems

<table>
<thead>
<tr>
<th>Species</th>
<th>Growth form&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Ecosystem</th>
<th>C</th>
<th>N</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adenostoma fasciculatum</td>
<td>e</td>
<td>Chaparral</td>
<td>683</td>
<td>—</td>
<td>88</td>
</tr>
<tr>
<td>Arctostaphylos glauca</td>
<td>e</td>
<td>Chaparral</td>
<td>712</td>
<td>—</td>
<td>88</td>
</tr>
<tr>
<td>Heteromeles arbutifolia</td>
<td>e</td>
<td>Chaparral</td>
<td>688</td>
<td>14.2</td>
<td>85</td>
</tr>
<tr>
<td>Diplacus aurantiacus</td>
<td>d</td>
<td>Chaparral</td>
<td>732</td>
<td>15.5</td>
<td>85</td>
</tr>
<tr>
<td>Lepechinia calycina</td>
<td>d</td>
<td>Chaparral</td>
<td>692</td>
<td>22.3</td>
<td>85</td>
</tr>
<tr>
<td>Eriophorum vaginatum</td>
<td>g</td>
<td>Tundra</td>
<td>550</td>
<td>15.1</td>
<td>23</td>
</tr>
<tr>
<td>P. taeda</td>
<td>d</td>
<td>Tundra</td>
<td>520</td>
<td>—</td>
<td>88</td>
</tr>
<tr>
<td>Pinus taeda</td>
<td>g</td>
<td>Forest</td>
<td>636</td>
<td>—</td>
<td>23</td>
</tr>
<tr>
<td>Zea mays</td>
<td>g</td>
<td>Crop</td>
<td>520</td>
<td>—</td>
<td>114</td>
</tr>
<tr>
<td>Raphanus raphanistrum</td>
<td>f</td>
<td>Ruderal</td>
<td>560</td>
<td>52.4</td>
<td>86</td>
</tr>
</tbody>
</table>

<sup>a</sup>Growth form of each species is indicated as e, evergreen shrub; d, deciduous shrub; g, graminoid; or f, forb.

expensive constituents (the sum of the amounts of protein, lipid, and lignin) remains relatively constant. For example, among plant parts, leaves are high in protein and low in lignin, whereas roots and stems have the converse composition (23, 86, 88). Among species, those adapted to dry or infertile soils often produce evergreen leaves with low protein content and high lignin or resin content, the latter to deter herbivores (18, 90, 105). The inverse relationship between protein content and concentration of other energetically expensive constituents (e.g. lignin, lipid, and resin) across species and across plant parts results in a relatively constant carbon cost of synthesis. This conclusion differs from the common assumption that evergreen leaves are more expensive than deciduous leaves because of higher lignin and resin content (105, 121).

The respiratory cost of maintaining tissue is assumed to be determined primarily by the rate of protein turnover and rates of ion flux (1, 114). However, tissues with high protein content—a good predictor of protein turnover rate—or high rates of ion flux (e.g. leaves or fine roots as compared to stems or large roots) tend to be short-lived (116, 154). Leaves with high nitrogen content have more rapid turnover than low-nitrogen leaves both within and among species (27, 135, 136); roots of species with rapid nutrient uptake rates have higher turnover than roots of species with low uptake rates (25, 148). Consequently, total maintenance respiration integrated over the tissue lifetime may not vary greatly among tissues and species (S. Gulmon, H. A. Mooney, unpublished information).

In summary, although species adapted to different environments or plant parts of a given species differ strikingly in chemical composition, this may not be strongly reflected in differences in carbon cost of growth and maintenance over the lifetime of the tissue.
In contrast to the cost of carbon, the nutrient cost of growth (i.e. nutrient concentration on a weight-per-weight basis) is generally twice as great for leaves as for roots (21, 128) and, for leaves, can range at least ten-fold (0.5−7% nitrogen) from low- to high-nutrient environments (41; C. Field, H. A. Mooney, unpublished information). The nutrient cost of growth is the inverse of nutrient-use efficiency (i.e. the amount of biomass produced per unit of tissue nutrient; 49, 153, 159). The instantaneous nutrient cost of growth, which reflects initial nutrient investment in new tissue (49, 159), can be increased over the lifetime of the tissue by exudation or leaching losses or can be reduced by retranslocation of nutrients from senescing leaves (cf section on Resource Loss, below). In nonstorage tissues most nitrogen (about 70%) is in protein. Other major nitrogen-containing fractions (amino acids and nucleic acids) are associated mainly with protein synthesis and are therefore correlated with protein content (22, 23; Table 2). Over the range of most natural conditions, increased nitrogen availability leads to parallel increases in all nitrogen-containing fractions in leaves (23, 152). Thus, the distribution of nitrogen among the major chemical fractions differs little qualitatively either among species or in response to variations in the environment (22, 23, 152). However, with abnormally high nitrogen availability, amino acids, nitrate, or alkaloids may accumulate as nitrogen storage compounds in leaves (cf section on Storage, above), and during water stress some species accumulate proline or nitrate as an osmoticaic (2, 143). Although the major nitrogen-containing fractions tend to occur in constant proportion to one another, concentrations of specific proteins differ substantially with plant part, species, and nitrogen status. For example, leaves have a large proportion of protein in photosynthetic enzymes, whereas roots have proteins associated primarily with metabolic and absorptive functions (41); C₃ species have a larger proportion of their nitrogen as ribulose-1,5-bisphosphate carboxylase than do C₄ species (113); expanding leaves have more biosynthetic and less photosynthetic enzymes than do mature leaves (21); and plants grown at low nitrogen availability have a larger proportion of leaf protein associated with tissue maintenance and structure than do high-nitrogen leaves that have high concentrations of photosynthetic enzymes (44). This effect of plant nitrogen status probably explains why the efficiency of nitrogen use for photosynthesis decreases at low−leaf nitrogen concentrations.

All species examined to date also show a similar phosphorus distribution among chemical fractions (mostly inorganic P, nucleic acid P, and ester P; see 6, 7, 20, 22, 23). As phosphorus status improves, the phosphorus fractions that increase most strongly in concentration are inorganic P > ester P > nucleic acid P > lipid P. Thus in contrast to nitrogen, phosphorus distribution among major chemical fractions is highly sensitive to plant phosphorus status.

In summary, for both nitrogen and phosphorus, the nutrient cost of growth increases at high nutrient availability because of the increasing concentration of
all nutrient-containing fractions, particularly those temporary storage products (inorganic P and nitrate) that are least central to metabolism. However, currently no evidence supports the hypothesis that, if grown under the same conditions, species adapted to different soil fertilities will differ in the efficiency of their nutrient use, either in distribution of nutrients among chemical fractions or in total tissue nutrient concentration (20, 27).

As with nutrients cost, the water cost to produce new biomass (i.e. the water content of tissues plus the water transpired during the assimilation of the carbon contained in the biomass) increases greatly in sites of increasing water availability (8, 45). Indeed, well over 99% of this water is expended in transpiration, so that water costs are determined primarily by patterns of stomatal control (cf 33, 145).

In summary, the nutrient and water cost of growth is least when these resources are scarce, a pattern similar to that described for costs of resource acquisition. This change in exchange ratios among resources brings the ratio of internal reserves to a balance more nearly optimal for plant growth (Prediction 5). In contrast, the carbon cost of growth may show less variation across environments with differing energy availability.

**Whole Plant Growth**

In a resource-rich environment, the cost of acquiring each resource is relatively low whereas, in a resource-poor environment, at least one resource will have a high exchange ratio (cf section on Resource Acquisition, above), so that the total cost of producing a unit of new biomass is high. For example, on infertile soils it is expensive to acquire a given unit of nitrogen in terms of carbon invested in both root biomass and respiration per mole of nitrogen absorbed. Consequently, the cost of producing any tissue containing nitrogen is high, and the maximum potential growth rate that can be supported in such an environment is low. Similar scenarios of a high cost of growth can be developed for low-light or low-water environments.

The high cost of growth in a resource-poor environment is reflected in low relative growth rates in plants adapted to these environments (27, 52). In young plants maximum potential growth rate varies ten-fold (22-270% per week) among species (54) and is higher in species adapted to resource-rich environments than in species adapted to the low availability of light (53, 75, 78), water (52), or nutrients (27, 31, 54, 123). In a resource-poor environment only a slow growth rate can be supported, and the total biology of the plant is geared to function effectively at this level of resource supply (14, 27, 52).

**Allocation**

Economic theory suggests that plants should adjust allocation so that all resources equally limit growth, i.e. until the ratio of the marginal product to
cost is equal for all resources (Prediction 3). Studies of allocation qualitatively support this prediction. Plants respond homeostatically to resource imbalance by allocating new biomass to acquisition of the resources that most strongly limit growth (27, 90, 147). Carbon stress resulting from shading, heavy fertilization, or above-ground herbivory causes a reduction in carbohydrates and an increase in nutrient content (18, 34, 35). Plants respond by producing proportionately more shoot and less root material (15, 17, 30, 35) and, in the case of intense shading or herbivory, by increased root mortality (24, 63, 161). The resulting decrease in root:shoot ratio reduces carbon stress and returns carbon and nutrient reserves to a balance that is more favorable for growth. Conversely, nutrient stress leads to low concentrations of limiting nutrients and to accumulation of carbohydrates. Plants respond by increasing proportional allocation to root growth (17, 27, 35), and this leads to a more favorable carbon/nutrient balance. Water stress can cause either an increase or a decrease in root:shoot ratio, depending upon the species and the severity of water stress (69).

At a more refined level, allocation is adjusted within roots or shoots in response to environmental stress so as to maximize efficiency for capturing the most strongly limiting resource. This corresponds to an equalization of the marginal product–per-unit cost (Theorem 3). For example, shade-intolerant species in response to shading show substantial elongation of the primary stem at the expense of lateral stem growth (68, 117), increased leaf area per unit weight (12, 13), and disproportionate reduction in growth of lateral fine roots (71). Nutrient- or water-stressed plants show greatest fine-root growth in zones of localized nutrient or water abundance (37–39, 42, 70). Moreover, photosynthesis and nutrient uptake are adjusted to maximize rate of acquisition of specific limiting resources (e.g. light vs CO₂, nitrogen vs phosphorus; cf section on Resource Acquisition, above).

Plants characteristic of resource-rich environments are generally highly plastic in their allocation in response to environmental stress (27, 52). This is the expected economic response to a situation where costs are highly variable rather than fixed. In such environments, resource availability is spatially and temporally heterogeneous, depending upon the degree of competition from other plants; thus, a highly plastic pattern of compensatory allocation enables the plant to dominate the limiting resource. For example, a large increase in allocation to shoot growth in response to shade may enable a seedling to overtop neighboring individuals. In contrast, plants respond to temporal heterogeneity by storing resources to cope with unfavorable periods (cf section on Storage, above).

Plants from resource-poor environments are less plastic in their allocation pattern, presumably because they chronically experience a homogeneous resource imbalance (i.e. resource costs are more nearly fixed). Thus, plants from
infertile environments have genetically fixed high root:shoot ratios; these ratios change relatively little in response to variation in environment (20, 27, 52). As a result of this low degree of plasticity, when the environment temporarily becomes favorable, the plant can fully exploit that environment through storage rather than by changing its allocation to some pattern that would be inappropriate for the normal condition.

**Tissue Turnover**

Because of the inefficiency with which resources are withdrawn from leaves and subsequently reutilized to support new growth (cf section on Resource Loss, below), prolonged tissue life is a major mechanism by which the efficiency of resource use is maximized in resource-poor environments. For example, plants growing in infertile bogs have relatively low instantaneous rates of photosynthesis per unit of leaf nitrogen, but have relatively long-lived leaves, and therefore, these plants can achieve a carbon gain per unit of leaf nitrogen similar to or greater than plants growing in more fertile sites (21, 129, 138). The importance of slow tissue turnover is indicated by the increase in abundance of evergreen species in low-resource environments (4, 27, 91); among graminoids and evergreen species, rate of leaf turnover declines in dry and infertile habitats (27, 73, 135, 136).

The high efficiency of resource use conferred by long-lived tissues is advantageous in resource-poor environments where scarce resources are expensive to acquire and where a rapid growth rate cannot be supported. Yet in a resource-rich environment, high efficiency of resource use confers little selective advantage, because resources can be acquired with minimal expense (cf section on Resource Acquisition, above), and effective competition with neighboring plants requires rapid flux of internal reserves into growth (126).

**RESOURCE LOSS**

Although the rate of resource loss is just as critical as acquisition for determining resource budgets of perennial plants, it has received relatively little attention from physiologists and ecologists. Resource loss can be minimized by retranslocation prior to senescence of a plant part. For leaves, the extent of retranslocation varies 0–30% for carbon and 0–70% (mean of about 50%) for nitrogen and phosphorus (22). Materials retranslocated from senescing leaves prior to abscission can be used to support subsequent growth. Large proportions of proteins, sugars, polysaccharides, soluble phenolics, nucleic acids, and amino acids are hydrolyzed and retranslocated prior to senescence, but generally structural materials (cellulose, lignin, etc), condensed tannins, and sometimes polysaccharides remain behind in litter (23; Table 2). The limited data currently available suggest that major nutrient-containing fractions (e.g. nucle-
ic acids, proteins, phospholipids) do not differ greatly in their degree of hydrolysis in autumn (22, 23; Table 2). Consequently, for nutrients the efficiency of retranslocation may depend more upon the process of nutrient movement from leaves prior to abscission than upon variation in hydrolyzability of different nutrient-containing compounds. Plants grown at low nutrient availability have low nutrient concentrations in mature leaves and litter and generally retranslocate a larger proportion of the initial nutrient pool than do plants grown on fertile soils (46, 87, 140, 150, 127; but see 9, 22, 139). Low concentrations of nutrients in litter result in a high efficiency of nutrient use in the production of biomass in infertile sites (153).

Leaching of nutrients from leaves is most pronounced in plants with high nutrient status (87, 149). Consequently, plants growing on fertile soils have a higher nutrient cost of producing biomass than would be suggested by tissue nutrient concentration because of both the low proportion of nutrient retranslocation and the high rate of leaching.

Other potential major avenues of resource loss from plants are root exudation and carbohydrate transfer to mycorrhizal fungi. Plants that are carbon-stressed because of shade or very high nutrient status have lower rates of sugar exudation from roots than do plants with large carbohydrate reserves (124). In addition, the extent of mycorrhizal infection decreases with carbon stress (101). The decrease in carbon loss via the roots increases the efficiency of carbon use in a low-carbon environment.

Most woody plants initiate more stems than can be supported by the average rate of resource supply. This loss of stems generally accounts for only 5–10% of total annual carbon and nutrient loss (e.g. 32). When environmental conditions are good, these stems are retained and increase the number of loci at which growth can occur. This is an example of how a small decrease in the efficiency of resource use under average conditions greatly enhances the capacity for resource acquisition (total flux) and growth under intermittent occasions when conditions are good. Rates of stem turnover are highest in species adapted to resource-rich environments because these species are selected to maximize rates of acquisition and growth (high flux) even at the expense of efficiency in resource use.

Leaves and branches may be shed when they experience a negative resource balance. This maximizes the overall efficiency of resource use by ensuring that those modules with the highest rates of resource acquisition are retained (93).

SEXUAL REPRODUCTION

Although inflorescences of some species contribute substantially to their own carbon requirements (156), resource allocation to sexual reproduction is less effective in gaining resources from the environment than is allocation to
vegetative organs. The analysis of life-history strategies suggests that allocation to reproduction is analogous to a high-risk investment in that it becomes a larger proportion of total investment under conditions of high resource availability. Short-lived species must realize a rapid return on their reproductive investment and, therefore, invest in reproduction at a younger age and under conditions of lower total reserve accumulation (i.e. higher risk) than do long-lived species.

The carbon and nutrient cost of producing reproductive structures is generally high because of their high concentration of nitrogen, phosphorus, and lipids. Because reproductive structures have a high resource cost and divert plant reserves from functions that could provide greater resource return to that individual plant (e.g. leaves or roots), they may substantially reduce the overall efficiency of resource gain and use by the plant. Generally the total allocation of resources to reproduction is much greater in resource-rich than in resource-poor environments, and this further increases the cost of resource use in resource-rich environments.

In resource-poor environments where survival itself is tenuous, allocation to sexual reproduction is relatively small in most years (142). In such environments, most reproduction occurs in mast crops, generally following a year of favorable conditions. Perhaps in species that gear vegetative growth and physiology to efficient but low rates of resource use, resource abundance that occurs only intermittently provides greater return when invested in reproduction than when invested in additional water or nutrient supply to existing biomass. In contrast, species typical of favorable environments have a more consistent allocation to reproduction.

SUMMARY

Our survey of the literature suggests that at least the vegetative growth of plants conforms closely to those theorems of economics that predict how profit should be maximized and resources optimally allocated. Plants do adjust phenology and life history patterns to acquire resources when they are cheap, to store these resources internally and to utilize them when conditions are most favorable for growth (Prediction 1). Plants apparently do continue to produce leaves (and perhaps roots) only until the marginal revenue from this increased production is equal to the marginal cost (Prediction 2). Plants adjust allocation so that their limitation of growth is more nearly equal for all resources (Prediction 3). This theorem describes growth in relation to resource limitations more accurately than does Liebig’s law of the minimum (i.e. that only one resource limits growth at any time). Perhaps the most interesting conclusion of this review is that plants adjust physiologically to changes in resource availability to reduce extreme exchange ratios (Prediction 5). Consequently the balance of internal
reserves within the plant approaches the proportions that are optimal for growth of most plants. We propose that the economic concepts developed here could provide a useful framework for integrating future studies of plant resource acquisition and allocation.

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