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THE MINERAL NUTRITION OF WILD PLANTS

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INTRODUCTION

Our understanding of plant mineral nutrition comes largely from studies of herbaceous crops that evolved from ruderal species characteristic of nutrient-rich disturbed sites (52). With the development of agriculture, these ancestral species were bred for greater productivity and reproductive output at high nutrient levels where there was little selective advantage in efficient nutrient use. This paper briefly reviews the nature of crop responses to nutrient stress and compares these responses to those of species that have evolved under more natural conditions, particularly in low-nutrient environments. I draw primarily upon nutritional studies of nitrogen and phosphorus because these elements most commonly limit plant growth and because their role in controlling plant growth and metabolism is most clearly understood (51). Other more specific aspects of nutritional plant ecology not discussed here include ammonium/nitrate nutrition (79), calcicole/calcifuge nutrition (51, 88), heavy metal tolerance (4), and serpentine ecology (133).

CROP NUTRITION

Nutrient Absorption

ROOT-SOIL INTERACTIONS The rate of nutrient absorption by a root depends upon both nutrient supply to the root surface and active absorption by root cortical cells. Nutrient supply to the root surface depends upon (a) soil solution concentration, (b) buffering power of the soil (i.e. capacity of soil exchangeable pools to replenish the soil solution as nutrients are absorbed), and (c) rate of nutrient movement to the root surface by diffusion

or by mass flow of soil water. Nitrogen, phosphorus, and potassium are so dilute in the soil solution that mass flow of soil water to meet transpiration losses provides only a small part of the total plant requirement. Consequently, the bulk of these elements moves to the root surface by diffusion (55, 125, 132). Ions that readily adsorb to soil (phosphate \gg ammonium \gg potassium) have such low solution concentrations even in bulk soil that diffusion is frequently the rate-limiting step in absorption by plant roots. As soil solution concentration increases, root absorption capacity (i.e. absorption rate per unit root measured at a standard solution concentration) and temperature become increasingly important relative to diffusion in controlling nutrient acquisition by plants.

Calculations by Nye and others (6, 124, 125) indicate that for phosphate, ammonium, potassium, and nitrate, diffusion to the root surface is much slower than the absorption rate necessary for optimal growth. The far-reaching implication of these calculations is that kinetic properties of nutrient absorption by roots exert only minor influence over nutrient acquisition by plants except under conditions of luxury consumption; i.e. under even mild nutrient limitation, soil processes are the primary control over nutrient absorption by each unit of root. Nye's conclusion is based upon a comparison of nutrient diffusion rates in soil and nutrient absorption and growth rates of plants grown at low nutrient solution concentrations (25, 98). A simulation model based upon this information predicted well the total phosphorus absorbed from soil by a species with low root absorption capacity (onion) but underestimated the phosphorus absorbed by rape, a species with high root absorption capacity, particularly at high soil phosphate levels (26). This suggests that either rape increased solution phosphate concentration at the root surface (26) or that root absorption capacity is more important at low solution concentrations than predicted. Differences in efflux rate among species and treatments could also affect net nutrient absorption from soil. In natural situations, soil cracks, dead roots, and other inhomogeneities of soil may be extremely important in supplying nutrients to the root surface and overcoming diffusion limitation, particularly after rain. The relationship between nutrient supply by soil and nutrient absorption by plants is clearly an important area for future research.

Highly mobile cations like calcium and magnesium move readily to the root surface by both mass flow and diffusion and often accumulate around the root when supply exceeds absorption (124, 125). For these elements, active absorption by roots or passive accumulation in the transpiration stream is generally the rate-limiting step; and these elements limit plant growth only at extremely low bulk soil solution concentration or where roots absorb most nitrogen as NH_4^+ and absorb other cations at very low rates owing to charge imbalance (79).

ROOT CHARACTERISTICS Root absorption capacity is the absorption rate per unit root measured under standardized conditions of concentration, temperature, etc. Root absorption capacity differs among species (123) and varieties (35–70% heritable) (59, 97, 122, 167). Varieties and species with low relative growth rate generally have a high root:shoot ratio (28, 122) and low root absorption capacity (87, 97, 122). This large genetic variability in nutrient absorption and other nutritional characteristics and their relatively high heritability indicate the potential for natural and human selection (51, 59).

The rate of nutrient absorption depends upon concentration in the external solution so that plant nutrient status declines as the solution concentration of a given nutrient declines at the root surface [(51); Figure 1]. Roots respond to a lower shoot nutrient status (38) in compensatory fashion by developing a higher root absorption capacity for that specific nutrient (46, 49, 79, 85, 97, 130). Analogously, acclimation to low root temperature with consequent reduced absorption causes increased root absorption capacity (29). The observed 1.7- to 7-fold compensatory increase in root absorption capacity when roots are grown at greatly reduced nutrient concentration does not fully compensate for reduced availability, so tissue nutrient concentration declines. Similarly, because there is incomplete compensation in root absorption capacity for changing nutrient availability, high nutrient availability in soil leads to nutrient accumulation above levels that immediately promote growth (luxury consumption) (51).

Rate of absorption of one nutrient frequently depends on concentration of other elements in the soil solution and in the plant. For example, improved plant nitrogen status causes up to a 10-fold increase in root absorption capacity for phosphate (42, 154, 172) and vice versa (83, 176). Other ionic interactions involve competitive inhibition of ions for the same carrier site (e.g. between K^+ and NH_4^+) (51, 79) and cation-anion balance. For example, species that normally absorb nitrogen as NO_3^- , including most crops, fail to absorb adequate metal cations when supplied with NH_4^+ rather than NO_3^- and exhibit Ca and Mg deficiency symptoms (79).

INFLUENCE OF SHOOT Above-ground environmental conditions leading to rapid biomass accumulation also result in a high root absorption capacity (41, 42, 131, 172), as would be expected from the rapid mineral accumulation in new plant biomass in rapidly growing plants despite a generally low root:shoot ratio. Shoot demand is particularly important in determining root absorption capacity in fertile soils where water and above-ground environmental conditions become the primary environmental factors regulating growth. It is unclear whether enhanced absorption by rapidly growing plants results from: (a) more rapid rates of photosynthesis,

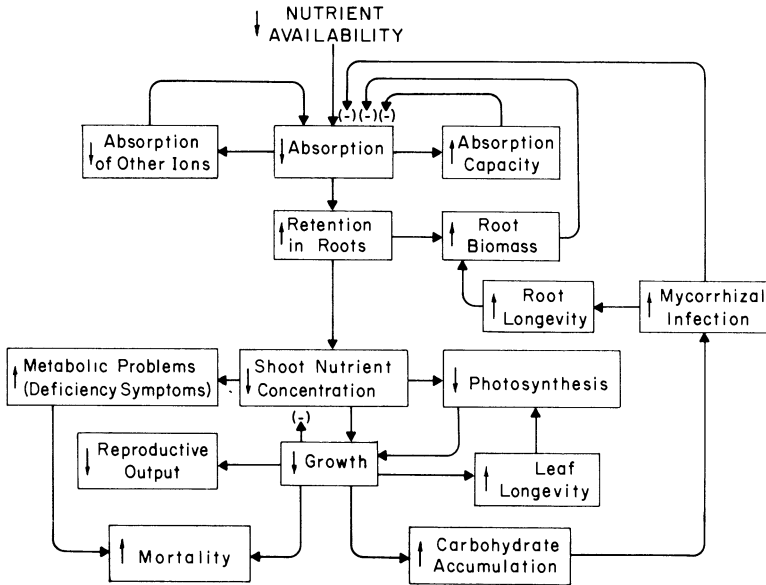


Figure 1 Response of crop plants to decreased availability of a single mobile nutrient. Vertical arrows inside boxes indicate an increase (↑) or decrease (↓) in the parameter. Arrows between boxes indicate a positive effect unless otherwise indicated (-).

sugar translocation to roots, and root respiration (41, 131); (b) increased nutrient demand by the shoot, translocation of inorganic nutrients out of roots, and consequent release of absorption processes from feedback inhibition (61, 172); or (c) synthesis of more carriers.

Allocation

In response to reduced nutrient status at low nutrient availabilities, reserves are allocated to root growth at the expense of shoot growth (Figure 1). A 100-fold drop in availability of a limiting nutrient causes a 1.5- to 12-fold increase in root:shoot ratio, depending upon species and initial growth conditions (25, 28, 37, 44). The combined compensatory effects of increased root:shoot ratio and increased root absorption capacity do not fully compensate for reduced nutrient availability, so that concentration and total quantity of nutrients absorbed by the plant generally decrease with decreasing availability (164).

The mechanism by which root:shoot ratio increases in response to reduced nutrient status remains unclear. Brouwer (28) suggested that because root meristems are closer to the nutrient supply, they receive a disproportionate share of nutrients and consequently grow more rapidly than shoot

meristems until the nutrient:carbohydrate ratio increases to the point where carbohydrate becomes more limiting to growth. Then shoot meristems, being closest to the source of carbohydrate, grow disproportionately. This hypothesis is supported by the tendency of a limiting nutrient to be retained within the root system of many species to a greater extent at low than at moderate-to-high availability (25, 98, 154, 176; but see 40). Although Brouwer's hypothesis is not entirely consistent with experimental evidence (40, 161), it is the framework for several simulation models of plant growth that accurately predict distribution of nutrients and carbohydrates between roots and shoots (6, 157). The role of hormones in regulating root:shoot ratio in response to changing nutrition remains unclear (104, 168).

A 2- to 3-fold variation in soil solution nutrient concentration within a few centimeters is not uncommon (147). Plants exploit pockets of high concentration of a limiting nutrient by localized proliferation of lateral roots in zones of high availability, combined with a corresponding decrease in allocation to other parts of the root system (48, 49). Thus, reduced plant nutrient status results in greater allocation of reserves to root growth, and this root growth is concentrated in zones of high availability of limiting nutrients.

Once within the shoot, mobile nutrients (nitrogen, phosphorus, and potassium) move preferentially to sites of greatest meristematic activity or "sink strength," as determined by growth form and growth stage (96, 104, 169). Thus, reduced nutrient status has much less effect upon leaf number and size in the apical shoot than upon the size and number of lateral shoots or tillers produced (63, 96, 104, 169). Hormonal balance probably exerts primary control over nutrient distribution within the shoot (168), though there is also evidence for a primary role of mineral nutrition in apical dominance (104).

Species in which leaf number per shoot is determinate show large variations in leaf size (86), whereas species with a variable leaf number generally respond to improved nutrient status primarily through a change in leaf number (9). In forage grasses, elongation of a new leaf occurs only after complete expansion of the previous leaf and is generally accompanied by senescence of an older leaf. Thus, although rate of leaf production may vary, the number of physiologically active leaves remains nearly constant over a broad nutritional range (96, 108). Leaf size of forage grasses, particularly in later leaves which have the most cells, is highly responsive to nutritional status (108).

Macronutrients differ in their effects upon growth. Of the mobile elements, nitrogen generally has greatest effect upon growth, affecting cell number and cell size; phosphorus has similar but less pronounced effects;

potassium has least effect upon growth, affecting mainly cell size (96, 169). Relative effects vary greatly, of course, depending upon availability and specific plant requirements. In contrast to the mobile nutrients N, P, and K, calcium, which is immobile in the phloem, accumulates in the xylem and at sites of maximum transpiration. It moves less readily to the meristem and may restrict meristematic activity more than expansion and activity of older leaves (51).

Response to Nutrient Stress

If nutrient supply from soil is insufficient for growth, nutrients that support continued growth of meristems and young leaves come from older leaves (176, 177), where they are removed primarily from inorganic storage pools in vacuoles and to a lesser extent from readily hydrolyzable compounds such as phosphate esters and amino acids (14, 24). This reduces rates of protein and chlorophyll synthesis, so that light-saturated photosynthetic rate declines [Figure 1; (24)]. Photosynthetic rate is proportional to leaf nitrogen concentration over a broad range, because the bulk of leaf nitrogen is directly involved in photosynthesis as a component of photosynthetic enzymes and chlorophyll (24, 114, 118). However, photosynthesis is progressively less responsive to changes in leaf phosphorus and potassium concentration (118, 153). Respiration rate, being roughly proportional to tissue protein content (129), also declines under nutrient stress (24, 139). Nutrient stress has a greater effect upon growth than upon photosynthesis and net assimilation rate, so that nonstructural carbohydrate concentrations rise above levels immediately needed for growth (51, 146, 169).

Leaf senescence is a common response to inadequate nutrient supply. When a leaf senesces, RNA, protein, and other N- and P-containing compounds are broken down to inorganic and soluble organic forms. Up to 90% of the maximum leaf N and P, 70% of the K, but none of the Ca is translocated out of senescing leaves before abscission (24, 176, 177). In cereals, root absorption capacity declines with age, and mobilization of nutrients from older senesced leaves provides the bulk nutrients in the grains (96, 130, 176, 177). Therefore, as plant nutrient status and the quantity of mobile nutrients in leaves decline, reproductive output declines.

If, following depletion of soil nutrients from the rhizosphere and senesced leaves, there are insufficient nutrients to maintain continued meristematic growth, the plant exhibits a variety of visible deficiency symptoms as well as greatly reduced rates of photosynthesis, respiration, and nutrient absorption (51, 78, 114, 118, 139). The meristem dies or becomes dormant, and the plant is no longer responsive to improved nutrient availability.

In summary, a crop species responds to a gradual decrease in availability of a single mobile nutrient first by a decrease in vacuolar reserves, reducing the accumulation due to luxury consumption and slightly reducing growth rate. The second stage involves continued reduction in tissue nutrient concentration, especially in older leaves and stems; reduced photosynthetic rate; reduced growth rate (mostly lateral branch growth and leaf expansion); increased nonstructural carbohydrate concentration; senescence of older leaves; lower reproductive output; and reallocation of reserves to compensate for reduced nutrient status (increased root : shoot ratio and root absorption capacity). The last stage of mineral deficiency reflects metabolic derangement with characteristic deficiency symptoms, greatly reduced photosynthesis, reduced root absorption capacity for all nutrients, and finally death or dormancy of the meristems. The degree of nutrient limitation can be recognized by the magnitude of the growth response when the limiting nutrient is added, which in turn can be predicted from tissue nutrient concentration (51, 65, 164).

NUTRITION OF WILD PLANTS

The nutritional characteristics of wild plants from fertile habitats are quite similar to those described above for herbaceous crops. Both groups of species exhibit the following traits: They have high relative growth rates that are quite responsive to nutrient supply (22, 37, 39, 70, 86, 117, 137). They respond to moderate nutrient stress in compensatory fashion by increased root absorption capacity for the limiting nutrients (19, 78), increased root:shoot ratio (37), decreased photosynthetic rate, visible deficiency symptoms, and decreased reproductive output (37, 39, 67, 137).

These nutritional responses differ considerably from those of wild species from less-fertile habitats. Although soil fertility is a relative term, and a species may be considered to be from a fertile or infertile site only with reference to the species with which it is compared, there are consistent patterns of nutritional response in plants from soils of differing fertility, as described in the remaining sections.

ADAPTATIONS TO NUTRIENT STRESS

Nutrient Absorption

ROOT ABSORPTION CAPACITY Compared with species from more fertile soils, slowly growing species characteristic of infertile soils usually exhibit a low absorption rate per plant and a small increase in absorption rate in response to increasing external concentration (17, 22, 37, 39, 88, 101,

137, 149, 171). Consequently, in comparison with species from high-nutrient environments, species from infertile soils absorb considerably less nutrient under high-nutrient conditions but similar quantities and in some cases even more nutrients at extremely low availability.

Root absorption capacity (per g root rather than total absorption per plant) is usually higher in rapidly growing species from fertile habitats than in plants from infertile habitats under all growth conditions (34, 37, 72, 78, 117, 148, 171) or only at moderate and high nutrient availabilities (149; but see 3, 8, 17, 36). These observations, based in most cases upon growth experiments, suggest that species from infertile habitats would generally have a lower V_{\max} and perhaps a lower apparent K_M of nutrient absorption than species from fertile habitats. Thus, in most cases plants have *not* adapted to nutrient stress through the evolution of an enhanced capacity to extract minerals from soil.

The apparent anomaly of low root absorption capacity in species adapted to nutrient-stressed sites is not surprising when considered in the context of the soil-root system. At low nutrient availability, nutrient diffusion to the root surface limits absorption, and even a low root absorption capacity is adequate to absorb those nutrients that reach the root (124, 125). Selection for high root absorption capacity should be strongest in moderate- and high-nutrient soils where diffusion is less important. In the absence of this selective pressure, a lower root absorption capacity with presumably lower protein requirement may be favored, particularly if absorption is effective at low concentrations (low apparent K_M). Moreover, plants with high absorption rates have high efflux rates (I. A. McPharlin, R. L. Bielecki, personal communication), so that a high absorption capacity may be disadvantageous at low nutrient availability. It is noteworthy that the evolutionary response of plants to low nutrient availability (low root absorption capacity) is precisely opposite to the short-term acclimation response by a single genotype (high root absorption capacity). Evolution apparently leads either to a rapidly growing type with rapid resource acquisition or to a slowly growing type with slow resource acquisition. The physiological adjustments then made by an individual are compensatory and change the rate of resource acquisition toward a level to which the genotype is adapted, as explained below.

ROOT:SHOOT RATIO Plants from infertile habitats maximize nutrient intake more through a high root:shoot ratio and mycorrhizal associations than through a high root absorption capacity, as predicted (124, 125). The high root:shoot ratio found in the field in many infertile habitats (47) is in part a phenotypic response to reduced nutrient availability (37, 98, 171). Rapidly growing species from high-nutrient habitats show considerable

phenotypic plasticity in root:shoot ratio and generally have a higher ratio at low availability and a lower ratio at high availability than do species from a low-nutrient habitat (37, 69, 171; but see 151). For example, root:shoot ratio varied 19-fold in response to altered phosphate nutrition in the rapidly growing *Cenchrus ciliaris* but only 2-fold in the slowly growing *Thyridolepis mitchelliana* (37). Similarly, low-P-adapted Australian heath plants showed no change in root:shoot ratio with changing phosphorus status (8). This is consistent with Grime's generalization that species characteristic of favorable habitats show greater plasticity in allocation pattern than do species from stressful environments (67, 68).

Although root:shoot ratios measured in the field are within the range of those measured in solution culture for species from fertile habitats, field root:shoot ratios of species from infertile habitats are about 5-fold higher than those measured in solution culture (29, 47), which suggests greater root longevity in infertile habitats. The limited evidence from root turnover studies is consistent with this hypothesis (142). Mycorrhizal associations, which are most strongly developed in infertile habitats and prolong root life (113), may be partially responsible for greater root longevity in infertile habitats. Roots with rapid turnover have high respiration rates (34). Because root absorption capacity generally declines with root age, the large root biomass achieved in infertile habitats, in part through increased root longevity, may be incompatible with a high root absorption capacity. In such diffusion-limited habitats, a large root biomass has greater value (124).

RHIZOSPHERE INTERACTIONS Mycorrhizal associations between roots and fungi are critical to plant nutrition in infertile habitats, as thoroughly reviewed elsewhere (14, 113, 125). The energy expended in support of mycorrhizal fungi is presumably less than that needed to produce an equivalent surface area of roots with their 10- to 100-fold greater diameter. Mycorrhizae provide the greatest benefit to plants in overcoming limitation by nutrients that diffuse slowly in soil (phosphate \gg ammonium \gg potassium $>$ nitrate). For example, transport of phosphate to the root surface via mycorrhizal hyphae can be 1000-fold faster than diffusion through soil (14). Mycorrhizal associations are best developed in infertile sites; but it is not known whether the species adapted to these sites have characteristics that promote mycorrhizal associations, though their slower root turnover favors mycorrhizal establishment. Certain families composed largely of ruderal species, the Cruciferae and Chenopodiaceae, have low degrees of mycorrhizal infection (84).

Plants can directly alter nutrient availability at the root surface by (a) secreting H^+ or HCO_3^- in exchange for NH_4^+ or NO_3^- , respectively, and changing rhizosphere pH by as much as 1 pH unit (26, 125); (b) secreting

oxygen into anaerobic soils, which oxidizes iron and reduces phosphate availability at the root surface; (c) solubilizing rock phosphate (95); (d) hydrolyzing organic phosphates with root surface phosphatases (14, 179); (e) fixing nitrogen; and (f) stimulating decomposition of soil organic matter in the rhizosphere through root exudation of soluble organic compounds (120, 125, 138). All of these changes in nutrient availability can greatly influence plant growth under infertile conditions, as discussed in the cited references. However, there is at present little evidence (owing perhaps to little study) that species adapted to infertile conditions are more effective than other species in increasing nutrient availability at the root surface. For example, crops and species from infertile soils have similar rates of root exudation (121) and root phosphatase activity (18, 179). Interspecific comparisons of processes altering root surface nutrient availability could greatly change present concepts of plant nutrition in infertile habitats (179).

SEASONAL PATTERNS Nutrient concentrations in soil solution and therefore nutrient absorption by plants fluctuate considerably during the year. In nonagricultural soils there is generally a predictable spring nutrient flush and in some areas also an autumn or winter flush associated with leaching and breakdown of fresh litter, a spring increase in microbial activity, and freeze-thaw or wetting-drying cycles that lyse microbial cells (7, 13, 74, 77, 89). Other less predictable flushes in nutrient availability occur at other times. In infertile habitats it is likely that a large percentage of annual nutrient absorption occurs during nutrient flushes (30), particularly during late winter or early spring (31, 111), rather than by steady-state absorption under average conditions.

Leaf Longevity

The most consistently observed characteristics of species from infertile habitats are traits that reduce annual nutrient requirement, principally increased leaf longevity and a low relative growth rate. Increased leaf longevity, associated with a lower rate of leaf production, is a phenotypic response to moderate nutrient stress in graminoids (96, 103) and evergreen trees and shrubs (35, 107, 151), though fertilization may actually increase leaf longevity of conifers in the first year of application (107, 163). Severe nutrient stress induces leaf senescence in all plants, but species adapted to infertile sites retain green leaves under conditions of lower nutrient availability than do species from fertile environments (69, 151). Evergreens become increasingly prominent on infertile soils, particularly on low-phosphorus soils (2, 10, 11, 99, 100, 109, 145, 170). Even within a growth form, species with greater leaf longevity tend to occupy most nutrient-poor sites (33). Several advantages of increased leaf longevity in nutrient-poor sites have been suggested:

1. Evergreen leaves may provide greater photosynthetic carbon return per unit nitrogen allocated to leaves than would deciduous leaves (111, 135, 141, 145). This hypothesis is based upon calculations by Small (145) relating photosynthetic rate to the average time that nitrogen is retained by leaves. These calculations have been questioned (32, 135), and in another site with similar species it was calculated that coexisting evergreen and deciduous species had similar carbon return per unit of nutrient invested in leaves (32). Small's hypothesis is important in suggesting a quantitative link between plant carbon and mineral budgets and deserves further critical examination.

2. Photosynthesis by long-lived leaves can meet plant energy requirements with little or no continued production, so that the plant can survive periods when there are insufficient plant nutrient reserves to sustain leaf production. Moreover, because of the inherent inefficiencies of nutrient retranslocation from senesced leaves (see below), plants with slow leaf turnover have lower annual nutrient requirements; this would be advantageous in an infertile habitat (32).

3. Evergreen leaves are less susceptible to leaching (43, 135, 162). However, the slow leaching rate of evergreen leaves is counteracted by the longer time that evergreen leaves are available to be leached, so that annual nutrient losses by evergreens may exceed those of deciduous species (155).

4. Deciduous species suffer most of their annual nutrient loss during autumn leaf abscission, and this nutrient pulse into the soil is susceptible to leaching. In contrast, evergreen leaves, which are shed more gradually through the year and decompose more slowly, are less likely to cause nutrient loss from the ecosystem (109, 155). Although this hypothesis describes important differences in nutrient cycling between evergreen and deciduous communities, it invokes group selection, because it cannot explain why a single individual growing in the community should be favored by the evergreen habit. Moreover, even most deciduous communities are quite effective in retaining nutrients returned to soil (30, 166).

5. Evergreen leaves provide a more favorable carbon balance than deciduous leaves in equable climates, where photosynthesis is possible during most of the year (110, 128).

Increased leaf longevity entails certain disadvantages. Photosynthetic rate declines with leaf age and is generally lower in evergreen than in deciduous species from the same environment (32, 110, 128, 145). Because evergreen leaves are a stable potential food source for herbivores throughout the year (54, 136) and because they contain a much larger proportion of the total plant nutrient capital than do leaves of deciduous shrubs (32), evergreen leaves are protected by high concentrations of anti-herbivore defense compounds (136), which are energetically expensive to produce. These defenses are best developed on infertile sites where plants can least

afford to lose the nutrients contained in leaves (105). (See Bryant & Kuropat, this volume.)

Growth Rate and Luxury Consumption

The predominance of ecotypes and species with inherently low relative growth rates in infertile habitats has been noted in graminoids (22, 23, 37, 39, 70, 82, 101, 126), forbs (70, 117, 137, 171), and woody species (70, 72, 151). In short-term growth experiments, species from infertile sites generally grow more slowly than species from fertile sites even at very low nutrient availability (12, 17, 22, 37, 39, 94, 101, 126, 149), though in some experiments species from fertile sites cease to grow under low-nutrient conditions (137). As nutrient availability increases, rapidly growing species from fertile sites, particularly C_4 species, respond with greatly increased growth rates, whereas species from infertile sites show less growth response but increase tissue concentrations (22, 37, 39, 72, 89, 98, 126, 137, 149, 171). The greater growth response to improved nutrient availability shown by rapidly growing species from fertile sites as contrasted with slowly growing species is also evident in field fertilization studies (80, 90, 143, 150) and in their greater variation in growth rate among sites of differing fertility (150). Thus the major criterion for recognizing nutrient limitation in crops (i.e. a large growth response to addition of a limiting nutrient) is invalid and would give contrary results if different wild species, each growing in its normal habitat, were compared.

In a fertile habitat a high relative growth rate is clearly advantageous because it allows rapid production of leaf and root biomass which dominates available light, water, and nutrient resources. Several possible advantages of an inherently low growth rate in an infertile habitat have been suggested:

1. Slowly growing species may absorb nutrients slowly and therefore be less likely to exhaust available soil nutrients (39, 70). This hypothesis invokes group selection and is valid only at low root densities where roots of adjacent individuals do not compete. Except in disturbed or very fertile habitats, root competition is generally important, and individuals that deplete soil reserves more effectively than competitors should have an advantage.

2. Because only slow growth can be supported on infertile soils, a species with inherently low growth rate is functioning closer to its optimal growth and metabolic rate and may therefore be more fit in a low-nutrient environment than a rapidly growing species that experiences a 90% reduction in yield under the same infertile conditions (21). In other words, the entire physiology of the slowly growing species is adjusted to a low nutrient

regime, whereas that of the rapidly growing species is adjusted to higher nutrient availability and more rapid growth. Although this hypothesis is vague, it has considerable indirect support, as detailed in the following section.

3. Slowly growing species that absorb nutrients in excess of immediate growth requirements (luxury consumption) during nutrient flushes may use these reserves to support growth after soil reserves are exhausted (39, 68, 70, 137). A slow growth rate also extends the time that growth can continue on a given nutrient reserve and increases the probability of survival until the next nutrient flush. Slowly growing species from infertile sites maintain meristematic activity and the potential to respond to improved nutrition when subjected to nutrient stress (45), whereas meristems of rapidly growing species exhaust tissue nutrient reserves, differentiate, and can no longer respond to improved nutrient availability. Thus, owing to differences in length of growth period and survivorship under infertile conditions, a slowly growing species can produce more than a rapidly growing species over the annual cycle (39). This effect was clearly seen in a comparison between Australian heath plants and introduced species with higher phosphorus requirements when all species were given an initial phosphorus supply with no replenishment (151). All species absorbed most phosphate available to them in the first sample interval. The introduced species completed most of their growth during this time and showed considerable senescence before the end of the experiment, whereas native species continued to grow throughout the experiment, showed less senescence, and produced as much or more than the introduced species. Similar luxury consumption and prolonged seasonal growth are observed in other controlled growth experiments (39, 82) and in the field (111, 151). Luxury consumption and maintenance of inorganic phosphorus reserves by slowly growing species from infertile habitats are responsible for the high proportion of inorganic phosphorus and low proportion of structurally bound phosphorus characteristic of these species (117, 151). Many Australian heath species have large seed phosphorus reserves that, like luxury consumption, can support growth for many weeks with little or no absorption from soil (8, 72, 151).

Luxury consumption presumably occurs because there is only a limited change in root absorption capacity in compensation for changing plant nutrient status. This limited degree of compensatory change in root absorption capacity is advantageous in infertile sites because it allows effective exploitation of nutrient flushes. However, it is disadvantageous in fertile environments where it leads to toxic accumulations of nutrients and reduced growth and vigor (37, 71, 72, 80, 82, 115, 134). Toxic accumulations

of calcium by calcifuge species in high-calcium environments partially explain their poor growth in such environments (72, 88). Luxury consumption is most developed in slowly growing species because absorption rate under high-nutrient conditions differs less among species than does maximum relative growth rate (14).

Nutrient Concentration and Efficiency of Nutrient Use

A high efficiency of nutrient use could be an important adaptation to nutrient stress (59, 72, 98, 171, 172). However, this efficiency, generally defined as the quantity of dry matter produced per g nutrient, is simply the inverse of tissue concentration, and could be affected by several processes with quite different potential to contribute to future productivity, e.g. (a) luxury consumption and large vacuolar storage reserves [25–70% of total plant N and P; (14, 24, 79, 165)], (b) development of fiber and cuticular materials [25–85% of dry weight; (24)], or (c) accumulation of sugars and storage polysaccharides [1–45% of dry weight; (146)]. A more useful measure of efficiency might be respiration, photosynthetic, or net assimilation rate per g nutrient (145).

When grown under similar conditions, slowly growing species from infertile habitats generally have higher tissue concentrations (lower efficiency) of a limiting nutrient than do rapidly growing species (37, 39, 171; but see 72), suggesting that efficiency of nutrient use, as currently defined, is not an important adaptation to nutrient stress (39). At high availabilities, interspecific differences in tissue concentration are particularly pronounced and are due to luxury consumption by slowly growing species (39). At low availabilities, rapidly growing species often show very low nutrient concentrations associated with visual deficiency symptoms (39, 72, 98, 117, 137), reduced root absorption capacity (78), reduced respiration (27, 129, 139), reduced photosynthesis (27, 114, 118, 139), and increased mortality in response to other stresses such as drought (69) and disease. Rapid growth per se renders plants more susceptible to heavy metal toxicity (4), frost damage (1), hypersalinity, and drought (89, 90). In marked contrast, slowly growing plants from infertile habitats respond to nutrient stress by maintaining higher tissue nutrient concentrations, in part through luxury consumption and/or reduced growth rate, and show no visible macroelement deficiency symptoms (11, 39, 72, 117, 137), no large reductions in respiration, photosynthesis, or root absorption capacity (15, 16, 78, 82), and no pronounced vulnerability to other environmental stresses (69). These species apparently reach near-maximum metabolic rates at low tissue nutrient concentrations (8) and, for reasons discussed above, are able to maintain these concentrations under normal field conditions. The ability of slowly growing species to maintain metabolic effectiveness under conditions of

nutrient stress is a key adaptive feature that has received remarkably little attention.

When sampled under natural conditions, species from infertile sites generally have lower tissue nutrient concentrations than species from fertile sites, owing to reduced availability and absorption of nutrients (5, 20, 159). Low concentrations of nitrogen and phosphorus are not necessarily associated with low concentrations of other elements (57, 60, 99). Low tissue concentrations are the norm for these species and are associated with more structural tissue (often sclerophyllous leaves) (10, 11, 76, 99, 100, 110, 128), more accumulated nonstructural carbohydrate (146), and lower protein and chlorophyll content (99, 145). Because sclerophytic leaves contain less photosynthetic machinery and conduct CO₂ less rapidly (110, 128, 141), plants in infertile sites have lower rates of photosynthesis and growth.

Tissue nutrient concentrations sampled from natural vegetation generally differ less among sites than do soil nutrients, because the more rapid growth in fertile sites dilutes the larger plant nutrient pool and perhaps because of greater luxury consumption by species adapted to infertile sites (5, 20, 50, 76, 175). Consequently, tissue nutrient concentrations of wild plants are less sensitive indicators of soil nutrient availability (165) than in crop species (65, 164), owing to greater variation of wild plants in inherent growth rate, less growth response to nutrient availability, a smaller range in tissue nutrient concentrations (particularly at the high end of the scale), and greater environmental heterogeneity. Intraspecific variation in tissue nutrient concentration over a range of sites has been used as a measure of the nutritional niche breadth of the species (50, 58, 178). However, this measure ignores differences in growth among species that dilute their nutrient capital to differing degrees (143) and may be a less suitable measure than direct soil analysis (with its problems of interpretation) or a combined measure incorporating tissue concentration and production.

Storage and Seasonal Nutrient Changes

Infertile habitats, which can support only a slow growth rate, are dominated by perennial rather than by annual species (70). Seasonal storage of minerals and carbohydrates in nonphotosynthetic tissues is an essential feature of deciduous perennials. Their rapid spring growth is supported more by stored nutrients than by concurrent absorption, as shown by isotope studies and by the tendency of growth responses to fertilization to occur in late season or in subsequent years rather than in spring (75, 160). Moreover, the spring increase in leaf nutrient capital coincides with decreasing pool sizes of nitrogen and phosphorus in stems and large roots. Stem nutrient capital is gradually replenished during summer by absorption from soil and in autumn by translocation from senescing leaves (32, 66, 140, 152, 160).

Nutrients translocated from leaves move into developing fruits or support root growth as well as replenishing stores. Because of the asynchrony of growth of different plant parts, the same nutrient capital can serve several functions during the growing season (32).

The seasonal decline in nitrogen, phosphorus, and potassium concentrations in leaves of deciduous species is due initially to the diluting effect of cell wall material being accumulated more rapidly than cell contents and later to translocation of nutrients out of leaves (32, 64, 66, 73, 102, 127, 165, 173). Much of the potassium is removed by leaching (112, 162).

In contrast to deciduous perennials, evergreen species retain leaf nutrients in situ during winter rather than translocating them to stems or roots, so the seasonal decline in nitrogen and phosphorus concentrations in these species is due entirely to dilution by cell walls. In subsequent years evergreen leaves may retain stable concentrations and pool sizes of nutrients (32, 135) or temporarily gain nutrients owing to luxury consumption during nongrowth periods (111). Leaf and shoot growth of evergreens begins later and occurs more gradually than that of deciduous perennials and thus could be supported by direct absorption from soil or following short-term storage in leaves after autumn or winter absorption (32, 106, 111, 119). Fagerström and Lohm (53) review evidence indicating that in conifers added nitrogen moves primarily to leaves in the first season, where it presumably promotes leaf growth and photosynthesis; only in subsequent years is stem and wood growth enhanced. Thus as sites of nutrient accumulation and storage in evergreen species, leaves appear to be at least as important as roots or stems.

The accumulation of nutrient stores during winter enables the plant to grow when water, temperature, and radiation are most favorable for growth and buffers the plant from day-to-day dependence upon available soil nutrients (91). Thus seasonal nutrient storage, like luxury consumption, is essential to the success of perennial species in low-nutrient environments.

The relative abundance of various nitrogen- and phosphorus-containing compounds changes seasonally. RuBP carboxylase constitutes a larger percentage of the total leaf nitrogen of tundra graminoids at midseason than during the spring biosynthetic or autumn senescence phases (33). Chlorophyll-nitrogen becomes a smaller percentage of total nitrogen as Douglas-fir needles age (163). Inorganic phosphorus is a larger percentage of total leaf phosphorus in spring and autumn than at other times of year (56, 151). Phospholipids become a larger percentage of total phosphorus during winter in cold-hardy species (144, 181) and during vernalization of cereals (156, 174).

Storage of nitrogen and phosphorus during winter and times of luxury consumption occurs primarily as arginine and inorganic phosphate in va-

cuoles (14, 116, 152, 160, 165), except in several Australian heath species that store polyphosphate (91, 92) (perhaps an artifact of associated mycorrhizal fungi that store polyphosphate). Storage in mature plants thus differs from that in seeds where cells have no vacuoles and store osmotically inactive storage proteins and phytic acid (14).

Nutrient Loss

Adaptations that minimize nutrient loss, such as reduced leaching or more effective nutrient retranslocation from senesced leaves, have received less attention than adaptations related to nutrient absorption and growth. Leaching can cause substantial nutrient loss, exceeding seven times the maximum standing crop in shoots in the case of potassium, for example (162). In general, nutrients are leached in the order $K > N > P$, though the relative magnitude depends substantially upon plant nutrient status (162). Anything that reduces the water contact with leaves (e.g. well-developed smooth cuticle, certain types of pubescence, erect leaf angle, drip tips) reduces leaching loss. Sclerophyllous leaves with a well-developed cuticle are common in nutrient-poor habitats such as tropical rain forest (10, 11), chaparral (110), and tundra and bogs (135, 141, 145). Sclerophylly is a common phenotypic response to nitrogen deficiency in crops, and may have evolved in response to nutritional stress as much as to water stress in the above communities (10, 11, 99, 100, 110).

Leaching occurs most readily when there are high inorganic nutrient concentrations in the intercellular spaces of leaves, as during periods of rapid spring leaf growth or autumn senescence or in plants of high nutrient status (112, 162). Plants growing on infertile soils have lower concentrations of inorganic nutrients (14, 151) and lose less nutrient by leaching than do plants on fertile soils (107, 180). Leaves of plants on infertile sites can even remove nutrients from rain water (107, 155).

Half or more of the maximum nitrogen and phosphorus content of a deciduous leaf is translocated to other plant parts before leaf abscission (32, 56, 73, 107, 112, 151, 175, 176, 177), though some studies show no phosphorus retranslocation (93, 127, 158). Potassium is removed from leaves largely by leaching rather than retranslocation (32, 66, 112), and calcium, being immobile in the phloem, is not retranslocated at all (32, 51). Variations in extent of nitrogen and phosphate retranslocation depend upon plant nutrient status. Leaves with high nitrogen and phosphorus concentrations have a larger percentage of N and P in soluble and inorganic forms (14, 24) and retranslocate a larger quantity of N and P (per g dry weight) from leaves (12, 32, 107, 175). However, high-nutrient leaves also have less structural material per g dry weight, so the percentage nutrient content in

abscised leaves is higher than in leaves of plants with low nutrient status (12, 32, 81, 93, 107, 175). In general, plants of high nutrient status retranslocate a larger proportion of their leaf nitrogen and phosphorus than plants with low nutrient status (107, 163).

Measurement of the proportion of nutrients retranslocated depends upon initial nutrient status (as discussed above) and the state of the litter with which it is compared. Senesced leaves still remaining on the plant may not have completed retranslocation, but leaf litter on the ground is highly susceptible to leaching if not collected immediately after abscission. Species differ in extent of loss in leaf weight during senescence [0–40%; (32, 56)], so that an interspecific comparison of seasonal change in leaf nutrient concentration may not reflect equivalent differences in proportion of nutrients retranslocated. Plants with less structural tissue, generally those in more fertile sites, show greatest change in leaf weight during senescence, and proportional retranslocation by these species would be underestimated if changes in leaf weight are ignored. Keeping these difficulties in mind, species from infertile habitats (particularly evergreens) show greater differences in nutrient concentration between green leaves and litter (145, 151), smaller differences (32, 155), or no consistent differences (12, 56, 175) when compared to species adapted to fertile habitats. Estimates of extent of retranslocation range from 0–83% among wild species (32, 56, 62, 93, 112, 145). Clearly, effective retranslocation could be an important adaptation to growth in infertile sites and deserves critical study. The limited evidence available at present does *not* show that species adapted to infertile soils are particularly effective in retranslocating nutrients prior to leaf abscission.

Reproduction

Because of their slow growth rate, plants from infertile sites are generally long-lived and, compared to rapidly growing plants in fertile habitats, grow for a longer time before accumulating sufficient reserves to reproduce (68). Many of these species from infertile habitats reproduce abundantly only during widely spaced mast years, often following a year of favorable weather. Nutrient addition causes the same abundance of flowering, presumably because it allows more rapid accumulation of necessary reserves (63, 143). Nutrient stress delays reproduction.

Among species from fertile habitats, ruderal species such as annuals respond to nutrient deficiency by senescence of most leaves and translocation of most minerals and carbohydrates from leaves to inflorescences, as do cereals; whereas more long-lived competitive species respond to nutrient stress by reduced growth and reduced allocation to reproduction, in the fashion of forage grasses (67, 68, 151).

SUMMARY: PLANT STRATEGIES

Although there are many conceivable adaptations to improve plant nutrient status or efficiency of nutrient use in growth and reproduction, as described above, no species exhibits all of these traits, and indeed certain characteristics seldom occur together (e.g. high root absorption capacity and slow relative growth rate). There are, however, certain combinations of interdependent physiological characteristics that recur repeatedly in phylogenetically unrelated species and appear important in the successful exploitation of particular environments. These groups of physiological traits are the basis of the plant adaptive strategies described by Grime (67, 68). Grime provides evidence for three primary plant strategies in (a) stress-tolerant species characteristic of unfavorable (stressful) environments and in (b) competitive species and (c) ruderal species that characterize favorable habitats in which disturbance is infrequent or frequent, respectively. Thus, where light and water are not unduly limiting, extremely nutrient-deficient sites are dominated by slowly growing stress-tolerant species, nutrient-rich sites by rapidly growing competitive and ruderal species, and intermediate sites by a combination of the two and by plants with intermediate characteristics. This section summarizes information presented previously, emphasizing the interrelationships among characteristics that constitute either the stress-tolerant or high-resource (competitive and ruderal) strategies. These strategies are the endpoints in the spectrum of plant types that occupy the total range of soil fertilities.

Habitats of high and moderate fertility are most effectively exploited by competitive and ruderal species (including herbaceous crops), which have high relative growth rates (Figure 2). The root absorption capacity of these species is high, particularly at high external nutrient concentrations, and this provides the minerals necessary for rapid growth. The high root absorption capacity is sensitive to and depends upon a high photosynthetic rate because (a) plants in fertile soils have low carbohydrate reserves, and (b) these species have high root respiration rates. Competitive and ruderal species also have a high photosynthetic rate, which provides the carbon and energy for their rapid growth. This photosynthetic rate is, however, quite responsive to leaf nitrogen (and in some cases phosphorus) concentration, so that, if nutrient absorption is not maintained at substantial rates, photosynthetic and growth rates decline. Photosynthetic rate declines with leaf age and nutrient absorption capacity declines with root age, so that maintenance of both processes depends upon rapid (at least annual) turnover of both leaves and roots. These high rates of tissue turnover entail substantial nutrient loss in senesced tissues because of the inherent inefficiency of nutrient retranslocation. The high rates of carbon and nutrient acquisition

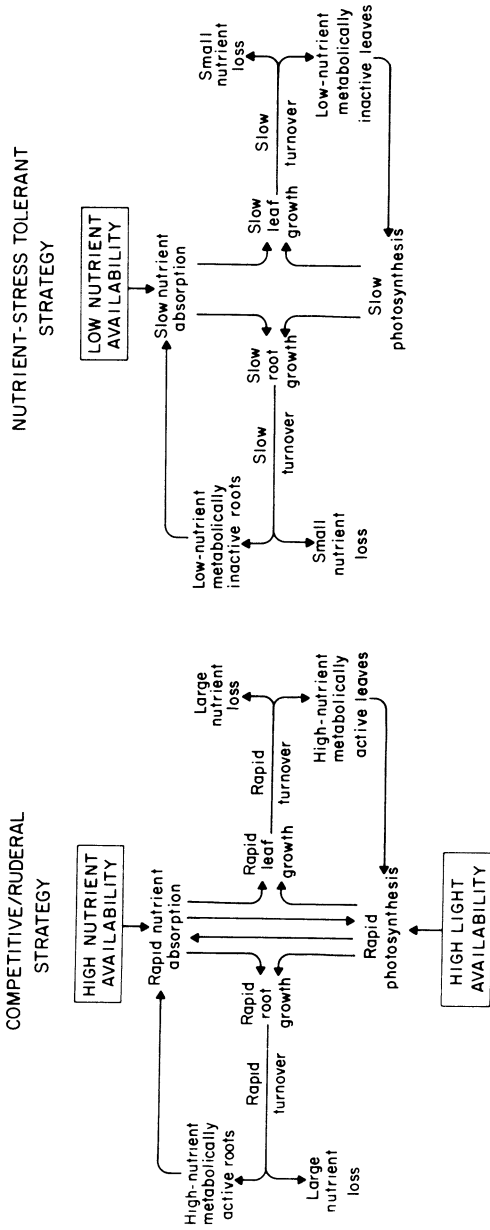


Figure 2 Interacting characteristics of plant strategies that are adaptive under conditions of high or low nutrient availability.

necessary to support the rapid growth of competitive and ruderal species are best attained in a fertile unshaded environment. In habitats of decreasing fertility, rates of nutrient absorption, photosynthesis, and growth decline, and plants exhibit deficiency symptoms and increased susceptibility to other stresses.

At the opposite extreme, infertile soils are most successfully exploited by stress-tolerant species whose inherently low growth rates can be adequately maintained by their low capacities for photosynthesis and nutrient absorption (Figure 2). A higher absorption capacity would provide little advantage in infertile soils, where diffusion of nutrients from bulk soil to the root surface is the step that most strongly limits absorption. These species maximize nutrient acquisition primarily by maintaining a large root biomass, and associated mycorrhizae, achieved in large part through slow root turnover. The long-lived nature of roots may in turn be partially responsible for their low root absorption capacity. The inherently low growth rates and the relatively small growth response to flushes of higher nutrient availability enable the plant to acquire and maintain nutrient reserves and in this way survive periods of exceptionally low availability in soil. The annual nutrient requirements of these species are low because of (a) slow rates of tissue production and (b) low nutrient loss rates through both senescence and leaching. This in large part explains the success of slowly growing stress-tolerant species on infertile soils. In response to declining nutrient availability, tissue reserves and growth rate decline slightly, but the normal metabolic effectiveness is maintained. Because of higher survivorship and the longer time that growth can be maintained on limited plant nutrient reserves, stress-tolerant species outproduce competitive species on infertile soils over the annual cycle.

Plants adapted to other stresses such as drought, salinity, shade, and low temperature also grow slowly and share many of the basic characteristics of plants adapted to infertile soils, reinforcing the concept of interdependent physiological characteristics constituting a stress-tolerant adaptive strategy. This is perhaps not surprising, considering that (a) nutrient and shade stress develop concurrently through succession (35, 67, 68) and (b) nutrient stress develops in most cold environments owing to reduced decomposition (30).

At a time when the agricultural trend toward use of high-yield grains with high fertilizer requirements is threatened by energy shortages and rising costs (and in many countries by scarcity of fertilizer), it may be necessary to breed crops with somewhat lower growth and reproductive rates but with lower nutrient requirements (51, 59). More thorough study of the nutrition of wild plants would provide a basis for predicting the combinations of characteristics that allow effective exploitation of environments of differing fertility. Such knowledge is essential not only to agricul-

ture but also to our understanding of the ecological and evolutionary patterns in natural communities.

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