

Response at the Foliar, Tree, and Stand Levels to Nitrogen Fertilization: A Physiological Perspective

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ABSTRACT. Key issues involving the role of nutrition in tree growth processes are presented at three levels of biological organization: the organ, the whole plant, and the stand. At the organ or foliar level, the strong linear response between foliar nitrogen levels and photosynthetic potential has been hypothesized to be a universal response in plants. Data on forest species, especially evergreen conifers, suggest a more complex relationship. The relationship between the potential for foliage to retranslocate nitrogen during shoot expansion and foliage longevity is also presented at this level. At the tree level, two issues appear critical: Is foliar nitrogen content optimized throughout the crown so that maximum carbon gain is realized? How does nitrogen stress control the allocation of carbon to the roots? At the stand level, the impact of carbon going to structures other than the stem (i.e., fine roots) and the interaction between canopy nitrogen and stand leaf area are examined. The use of fertilizers and water as management techniques to enhance productivity is integrated into the discussion of these issues.

Both water and nutrients are environmental factors that limit tree growth. Water is more often studied despite the frequency of nutritional limitations. On most forested sites, the addition of a single limiting nutrient can dramatically increase productivity, growth, and survival. In fact, in experiments with fertilization and irrigation, irrigation alone frequently results in little or no response. Therefore, nutrients and water may have equal importance in limiting growth; furthermore, nutritional regimes are more easily altered in forests than water regimes.

Since nutrients are required to complete the life cycle of trees, it is not unexpected that forest growth is regularly limited by nutrient supply. Such limitations are caused by low nutrient availability in the mineral soil, which depends on weathering rates of the parent material, and on the rate at which nutrients bound in the organic matter are decomposed and mineralized. As a result, forest tree species and forest ecosystems have evolved mechanisms to enhance uptake, conserve nutrients, and minimize problems associated with inadequate nutrient supply. But when forest ecosystems are disturbed

by fire, harvesting, or anthropogenic inputs, these mechanisms may be altered and growth reduced.

Allen et al. (1990) have discussed ways in which forest managers can improve site and stand productivity. First, the rate of site occupancy can be increased through genotype selection and site preparation, and through proper seedling conditioning, handling, and tending. Second, the maximum leaf area carried by a site can be increased through species/genotype selection (see also Leverenz and Hinckley 1990), reductions in competing vegetation, increases in the availability of existing resources, and additions of limiting resources. Nutritional management, including forest fertilization, is involved in several of the recommended steps. For example, through genetic selection, species or genotypes with superior nutrient use efficiencies or nutrient uptake capabilities may be used more effectively. Similarly, site preparation and subsequent vegetation management can be used to conserve nutrient capital as well as to control the rates of nutrient turnover (see Cole and Gessel, this volume). The changing rates of nutrient turnover and the vertical and horizontal extent of rooting can also have an impact on the uptake of nutrients by trees. In spite of the variety of ways in which foresters directly or indirectly affect site productivity, the addition of fertilizer remains the most frequently used technique.

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We discuss the importance to overall ecosystem nutrition of nutrient responses at the leaf, whole-tree, and stand levels, and the significance of conceptual and quantitative links connecting these three levels.

Perspective and Approach

Although many nutrient-related physiological processes are studied at the organ or cellular level, it is important that these processes be considered in relation to questions and issues at the whole-tree and stand levels. To do this, one must determine how process-

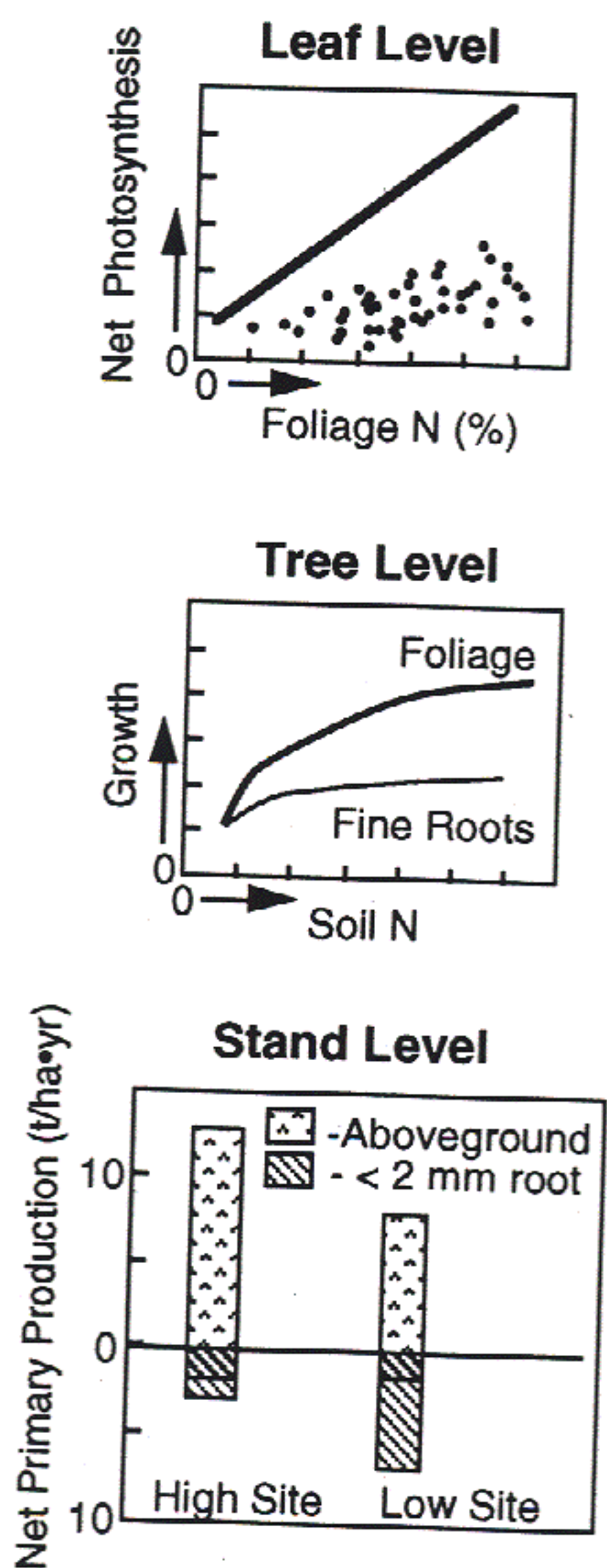


Figure 1. Three scales of biological organization that provide the framework for this chapter. Data for the graph at the top (leaf level) come from Field and Mooney (1986) (the solid line is for annuals and deciduous shrubs, while the dots illustrate the relationship for evergreen shrubs and trees); the center graph is from Friend (1988) and Friend et al. (1990); and the bottom graph is from Keyes and Grier (1981).

level studies can be linked and applied at larger spatial and temporal scales. Difficulties arise because of problems of integration and scaling from a lower (i.e., the leaf) to a higher level of organization (i.e., the stand). Integration is the summing of fluxes at one scale (e.g., nutrient uptake by all individuals on a given site) to provide an estimate of a flux at a larger scale (e.g., stand nutrient uptake) for a particular period. Unfortunately, the application of this approach is restricted because it fails to account for the negative feedbacks that result from competition when considering processes at a larger scale. Scaling involves the consideration of processes at successive levels of organization and explicitly addresses the negative and positive feedbacks that occur as the scale becomes successively larger (Whitehead and Hinckley 1991).

Because we are sensitive to the broader issues affecting forest managers, we have divided our presentation into three levels of organization: leaf, tree, and stand (Figure 1). We will deal with each of these levels in turn. In our presentation we will assume that water and nutrients are linked constraints and that carbon production and allocation reflect those constraints operating on specific processes within the tree. In other words, nutrient and water limitations are manifested through changes in both metabolism (e.g., photosynthesis) and growth (e.g., root-shoot ratios, biomass per unit land area). We will focus on nitrogen because it is most often the limiting nutrient in forest ecosystems.

Leaf Level

Figure 2 illustrates that leaf nitrogen can be allocated to a variety of functions within a leaf and that levels of nitrogen allocated to these functions may or may not result in the maximization of total leaf carbon produc-

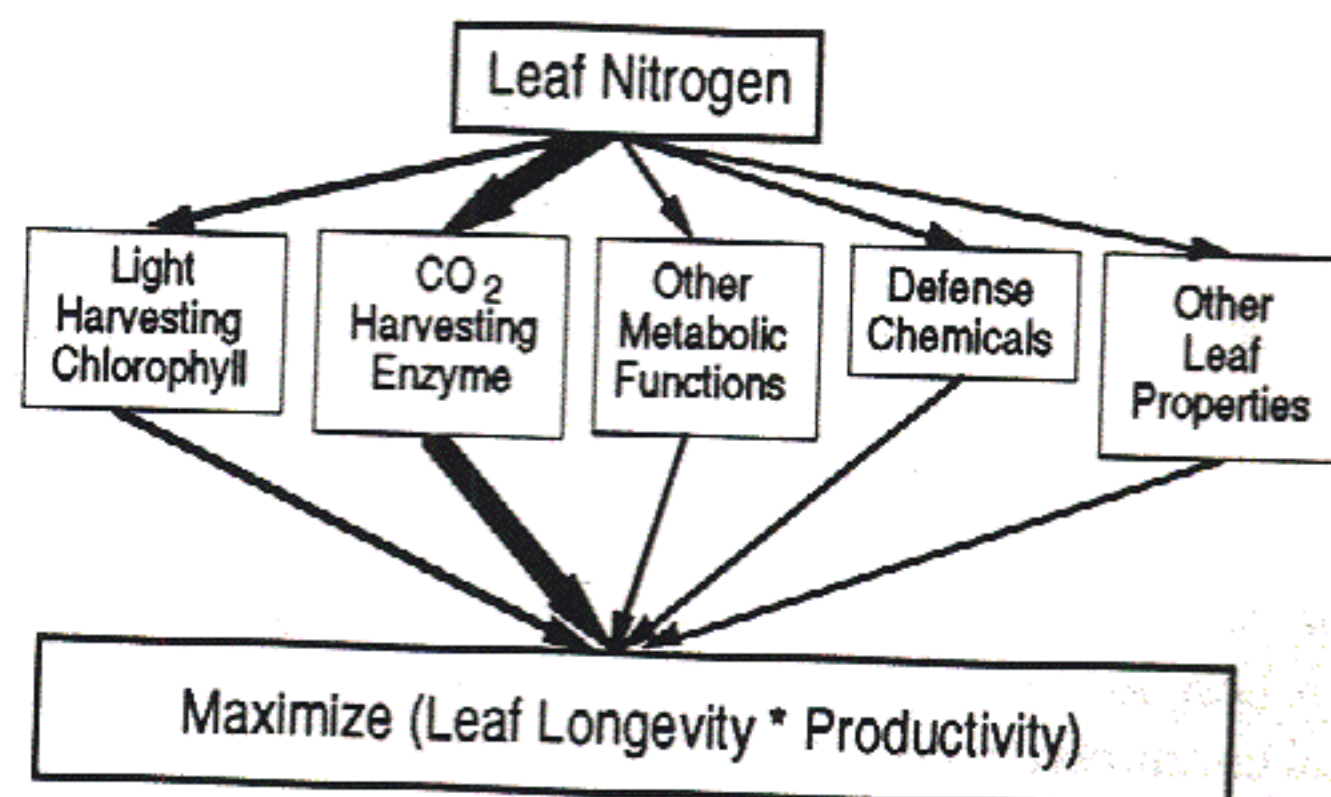


Figure 2. The potential ways that leaf nitrogen may be distributed within a leaf in order that the productivity capacity of the leaf will be maximized.

tion (the product of leaf longevity and the actual rate of net carbon fixation, less the initial carbon investment). The majority of leaf nitrogen is in proteins and most of that is in the enzyme Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase). This enzyme is responsible for the harvesting (i.e., fixation) of carbon dioxide in the dark reactions of photosynthesis. Thus a balance must be maintained between nitrogen allocation to harvesting light (i.e., chlorophyll) and nitrogen allocation to harvesting carbon (i.e., Rubisco). As an example of changes in nitrogen allocation within a leaf, Woodrow and Berry (1988) observed that as foliage became more shaded, the amount of total nitrogen allocated to chlorophyll increased.

Field and Mooney (1986) and Evans (1989) have shown that the variation in leaf nitrogen, mainly because of its role in Rubisco, can clearly explain much of the variation in photosynthetic capacity across a wide variety of plant life forms. Several authors have found a strong positive relationship between leaf nitrogen content, or concentration, and the maximum rate of net photosynthesis in woody plants, including conifers (Brix 1981; Hirose et al. 1989; Matyssek and Schulze 1987; Vapaavuori and Vuorinen 1989). In addition, changes in the patterns of leaf nitrogen allocation occur between sun and shade foliage; and also occur even within the leaf itself, as one goes from the top, sunny portion to the bottom or shady portion of the canopy or leaf (DeJong et al. 1989; Terashima 1989). In contrast to sun foliage, foliage in the shade has less nitrogen; and, of the nitrogen it has, more is allocated to light versus carbon dioxide harvesting (Seemann et al. 1987). It is unknown how leaf nitrogen allocation is altered to maximize net photosynthesis within a leaf (i.e., Figure 2) and between leaves as leaves age and/or become shaded. In some of the conifers, which retain foliage for as long as 5 (i.e., Douglas-fir), 20 (Pacific silver fir), or 50 years (bristlecone pine), retention, retranslocation, and reallocation of nitrogen must be important. In addition, the primacy of the relationship between leaf nitrogen and photosynthetic potential will depend on the relative limitation of other nutrients (Sheriff et al. 1986; Reich and Schoettle 1988).

Nitrogen availability may also affect the balance between the capacity of leaves to fix carbon (mesophyll or nonstomatal conductance) and the rate at which carbon, as carbon dioxide (CO_2), enters the leaf (stomatal conductance). This balance can be studied by examining photosynthetic responses to increasing experimental CO_2 levels and interpreted in the context of the relationship between the amount of CO_2 inside the leaf, c_i , and the rate at which the leaf uses that CO_2 , assimilation or A (Figure 3). These A/ c_i curves are a useful tool

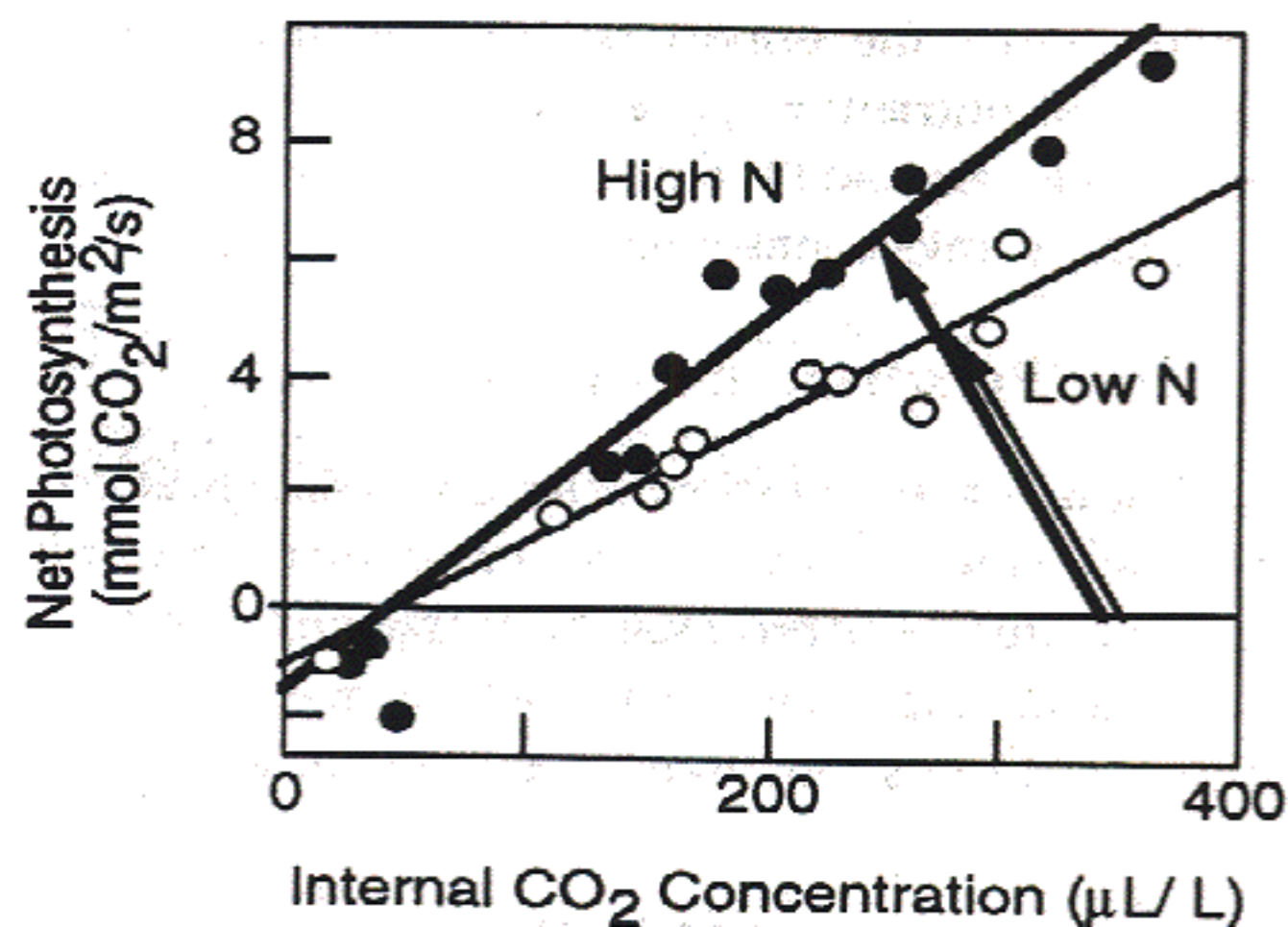


Figure 3. Relationship between internal carbon dioxide concentration and net photosynthesis (A versus c_i curve) in two different Douglas-fir trees. Foliar N was 1.58% in the high-N tree and 1.25% in the low-N tree (after Mitchell 1988). The two lines illustrate the gradient in carbon dioxide concentration between the outside and inside of a needle. External carbon dioxide concentrations were 360 $\mu\text{L/L}$.

because the initial slope of the response curve indicates the effect of N on fixation capacity, while N effects on stomatal conductance can be assessed by comparing the degree to which CO_2 inside the leaf is depleted with respect to the ambient atmospheric CO_2 level (340 $\mu\text{L/L}$). Figure 3, then, shows that the effect of foliar N on photosynthesis is primarily on the CO_2 -fixing capacity of the leaf, and not on the sensitivity of the stomata to CO_2 diffusing into the leaf. This effect on photosynthesis is the result of the increased level of Rubisco in the leaf (Mitchell 1988) that occurs in response to an increase in nitrogen supplied to the leaf (i.e., by fertilization).

These A/ c_i curves can also be used to speculate on the effects of anthropogenic increases in atmospheric CO_2 concentrations on the interaction between net photosynthesis, nutrient use efficiency, and water use. For example, since increasing ambient CO_2 will generally result in higher internal CO_2 levels, rates of photosynthesis would tend to increase and more carbon would be fixed. In contrast, stomatal conductance would not be affected, or would be decreased, by increased atmospheric CO_2 concentrations, and therefore increased water loss would not tend to accompany the higher photosynthetic rates. In addition, as CO_2 levels rise, rates of photosynthesis required for tree growth and development could be maintained with less Rubisco. Trees may then reallocate some of the nitrogen tied up in

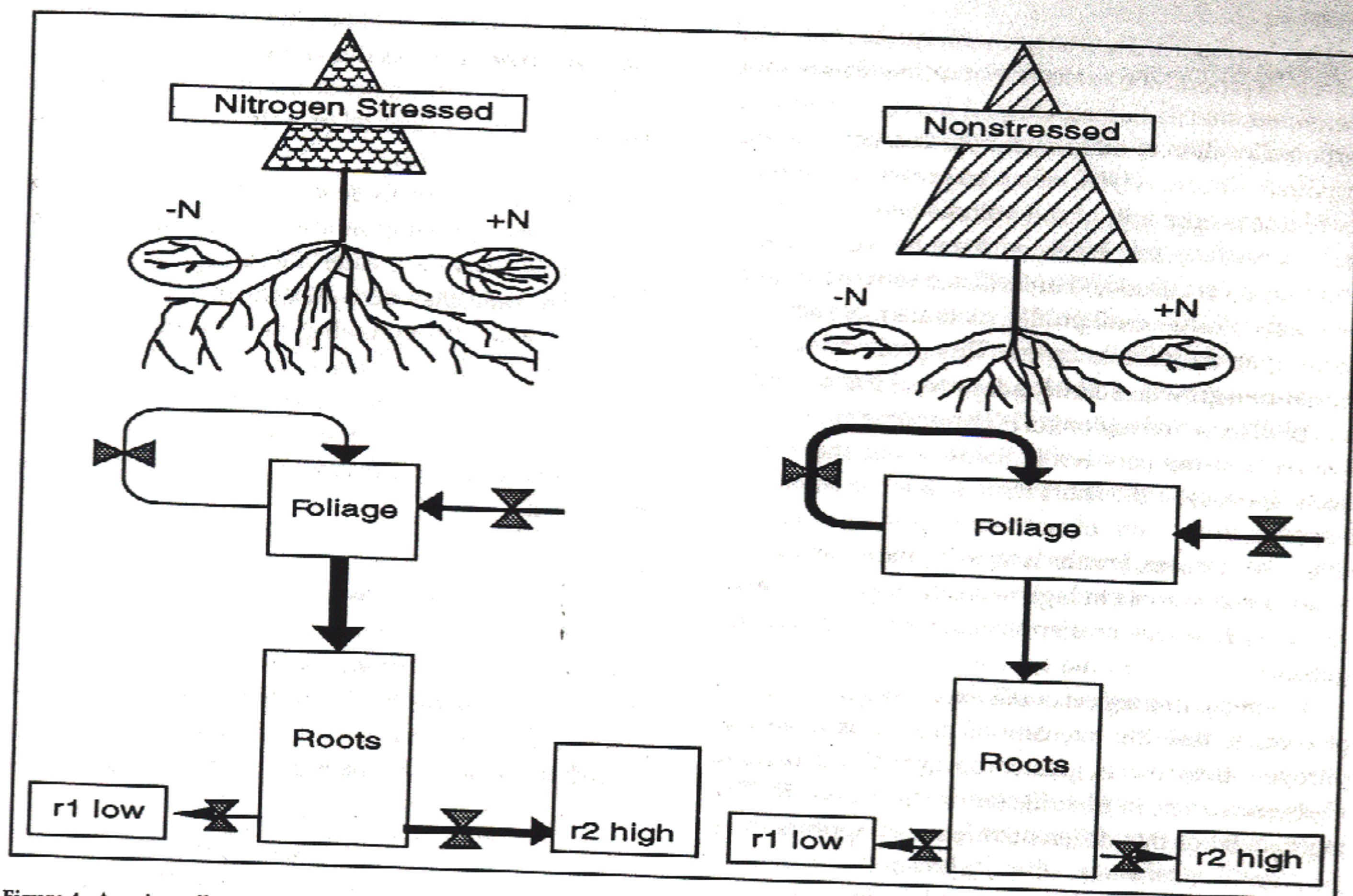


Figure 4. A carbon allocation model based on the results of a study of growth responses of seedlings and trees to differential root system and individual-root nutrient levels. The seedling study was conducted in a growth chamber (Friend et al. 1990) while the tree study was conducted in two 50-year-old Douglas-fir (*Pseudotsuga menziesii*) stands located 63 km east of Seattle, Washington. Stands were part of the Regional Forest Nutrition Research Project and had been maintained since 1969 (Friend 1988).

Rubisco to other leaf components, thereby increasing nutrient use efficiency.

Tree Level

Figure 4 illustrates the role of carbon allocation in compensating for a deficient supply of nitrogen. In general, leaf growth is more sensitive than root growth to water stress (Sharp and Davies 1989) and nutrient stress (Ingstad and Lund 1979; Friend et al. 1990). As a result, more carbon per unit of carbon fixed is used for root growth in low fertility than in high fertility soils. Increased carbon allocation to roots, under conditions of low water or nutrient availability, will maximize carbon gain because successful carbon investments into soil-resource capture will provide a positive feedback into carbon fixation by partly alleviating foliar stresses (Ledig 1983; Friend et al. 1990).

The relationship between nitrogen stress and carbon allocation in stand-grown trees is more complex than that in seedlings, for the following reasons: (1) nitrogen availability varies widely on temporal and spatial scales

in forest soils; (2) foliar growth is often restricted in time (i.e., a period typically less than the growing season) and space (i.e., canopy competition); (3) roots are growing in a competitive and heterogeneous environment; and (4) root growth must be evaluated over relatively long periods. Unfortunately, because the root systems of individual trees in stands can be differentiated only with great difficulty, information on individual-tree responses is inferred from seedling or whole-stand studies. In nitrogen-stressed trees, both shoot growth and net photosynthesis are reduced (Brix 1981a); however, shoots are more sensitive to nitrogen stress than net photosynthesis (Brix 1981b). This decreased shoot growth increases the availability of photosynthetically fixed carbon and results in a shift in allocation from shoots to storage products in stems or to fine root growth (Vogt et al. 1985).

Individual-root responses are of key importance to, and closely linked with, whole-tree responses. To understand the responses of fine roots, the heterogeneous nature of forest soils must be linked to the phenology of

the tree. Variation in fine root growth is probably caused more by temporal and spatial variation in soil properties (i.e., water, nutrients, temperature) than by variation in carbon allocation or other tree processes. For example, Friedman-Thomas (1986) observed greater variation in root biomass per unit of soil volume between surface and subsurface soil horizons than between similar horizons of fertilized and unfertilized soils in Douglas-fir stands. Within a soil profile, roots are more active in fertile than in infertile layers. This property of individual-root growth is clearly adaptive, as it allows roots to exploit localized regions of high resource availability. The relationship between individual-root and whole-tree responses in the short term is that the whole tree responds to the sum of nutrient acquisition from the entire root system. For the long term, more carbon will be allocated to roots in high resource areas and consequently whole-tree nutrient balance may significantly improve.

The intriguing aspect of this exploitive growth habit of roots is that the intensity of growth is related to nitrogen stress; that is, greater root growth will occur in N-stressed than in N-sufficient trees (Figure 5). The mechanism of this differential reaction appears to be

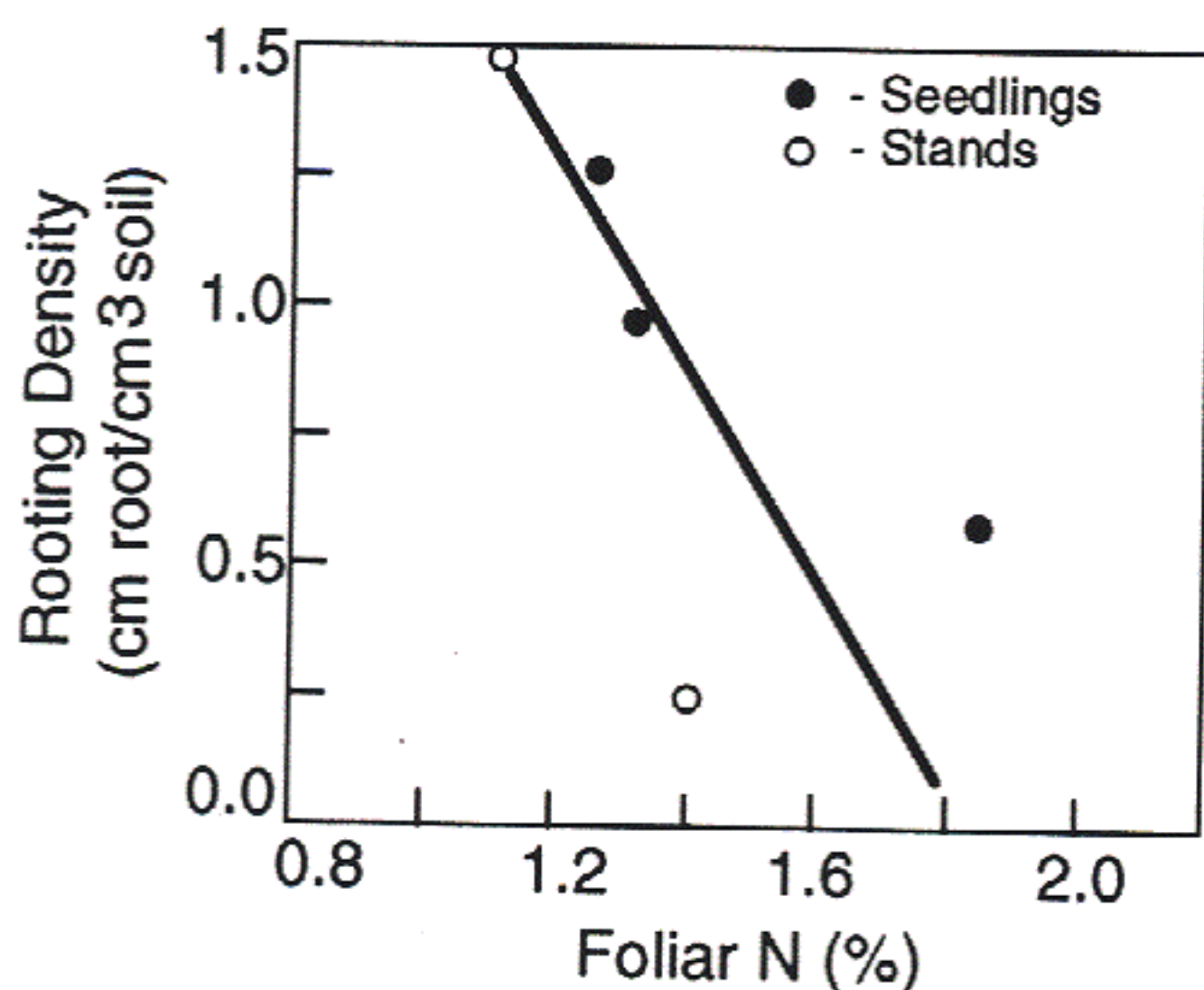


Figure 5. Generalized relationship between root proliferation in localized enriched regions of the soil and plant nitrogen regime for Douglas-fir seedlings (Friend et al. 1990) and 50-year-old Douglas-fir stands (Friend 1988). Root length was estimated from dry weight in each case using 30 m root/g dwt for seedlings and 50 m root/g dwt for stands (assumed: 0.5 mm diameter roots with densities of 0.1 g/cm³). Localized regions of high-N soil were provided by amending 0.4 L pots of a 50/50 v/v peat/vermiculite mix with solutions containing 100 ppm N as NH₄NO₃ for seedlings and by amending 0.9 L ingrowth bags of vermiculite with 9 mg N/g vermiculite as NH₄NO₃ for stands. Roots were allowed to grow for 75 days for seedlings and 180 days for stands. Foliage samples for N analysis were collected from stands in December 1986.

related to a change in root branching behavior. Roots of N-stressed trees, irrespective of the local soil environment, have a greater number of branches per unit length than those from nonstressed trees (Friend and Coleman 1989; Friend et al. 1990).

The integration of these concepts is illustrated in Figure 5. Trees growing in low-N soils (i.e., nitrogen stressed) will have a greater allocation, per unit leaf area, to fine roots than trees growing in high-N soils. In addition, roots of trees growing in low-N soils will grow more intensely when they encounter relatively resource-rich pockets than roots of trees growing in high-N soils (Figure 4). Both of these responses favorably channel carbon investments so that whole-tree carbon gain is maximized.

Stand Level

Grier et al. (1986) have demonstrated a strong relationship between nitrogen availability and the quantity of total net primary production allocated to fine root growth for the same species growing on different sites and for different ecosystems (Figure 6). However, Nadelhoffer et al. (1985) have questioned the validity of

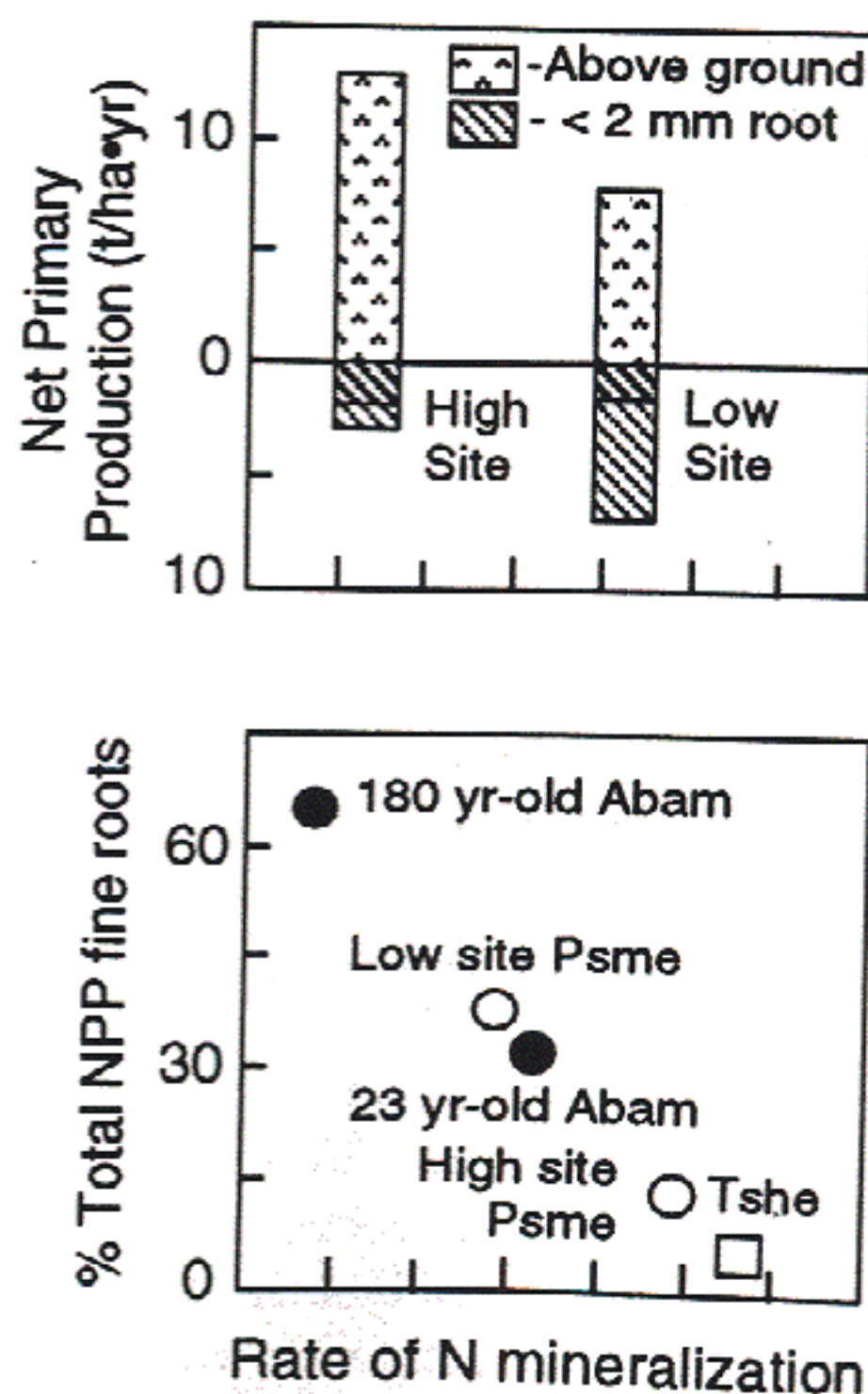


Figure 6. Top: Relationship between site and net primary production for 40-year-old Douglas-fir stands located at Pack Forest (Keyes and Grier 1981). Bottom: Relationship between the rate of N mineralization and percentage of total net primary production allocated to fine roots in 180- and 23-year-old Pacific silver fir (*Abies amabilis*) stands, low and high site Douglas-fir stands, and a young western hemlock (*Tsuga heterophylla*) stand (Grier et al. 1986).

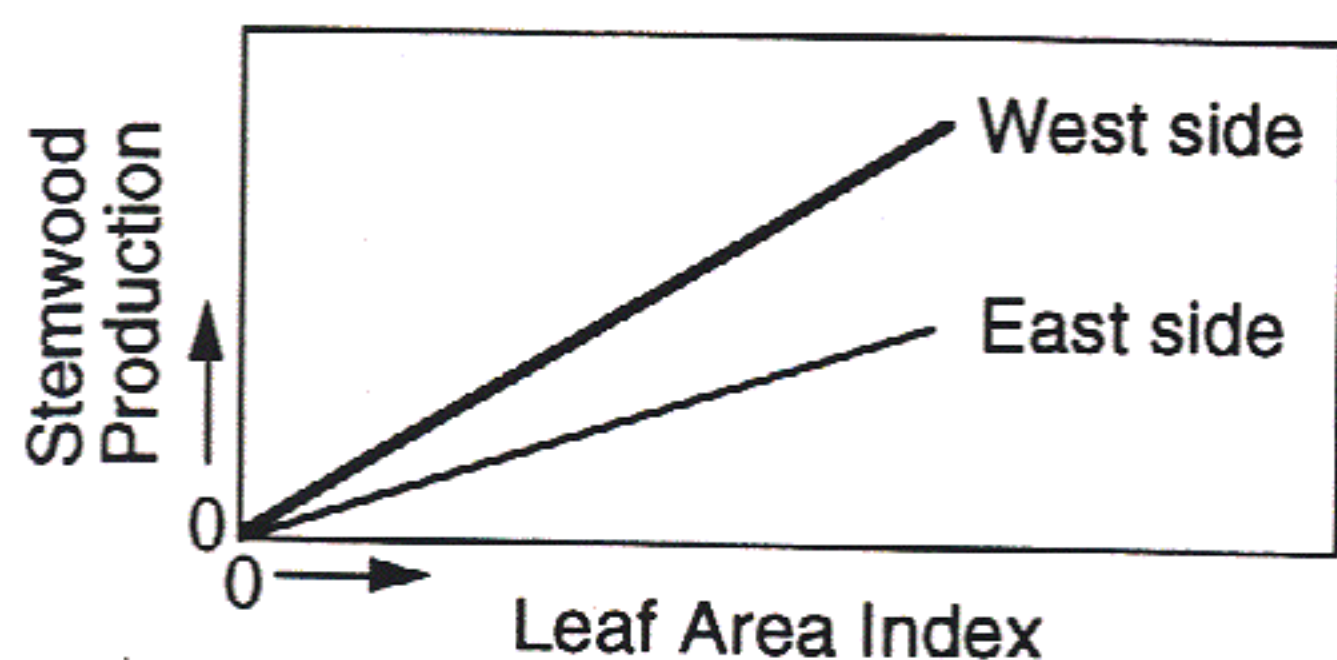


Figure 7. The relationship between leaf area index and stemwood production for Douglas-fir grown on the east and west sides of the Oregon Cascades (Waring 1983).

this relationship and have suggested that fine root production is actually greater in high-N than in low-N stands because of the greater rates of fine root turnover. This is a viable hypothesis but it relies heavily on indirect evidence for calculations. Until physiological and microbiological studies can support the assertions of Nadelhoffer et al. (1985) in the way our previous discussion has supported the hypothesis of Grier et al. (1986), an increase rather than a decrease in belowground productivity is the more logical explanation for observed root, tree, and ecosystem response to nutrient stress.

Independently of the role of site nutrient status in controlling the allocation of net primary production, many authors have focused on total light interception as the best indicator of net primary production and stemwood production (Waring 1983; Linder 1985; Cannell et al. 1987; Vose and Allen 1988; Pereira et al. 1989; Scarascia-Mugnozza et al. 1989; Colbert et al. 1990) (Figure 7). As shown in Figure 7, the shorter growing season of the east side of the Cascades reduces the amount of stemwood produced for a given leaf area index. As demonstrated by Vose and Allen (1988), fertilization and irrigation can increase the quantity of leaf area carried on a site; however, improving foliar nitrogen levels, at least in loblolly pine (*Pinus taeda*), will not improve stemwood production unless increases in leaf area index also occur.

Conclusions

We have demonstrated that processes on organ (leaf and individual root), tree, and stand levels are inextricably linked in determining tree responses to fertilization. It is clear that each level is affected not only by its environment but also by feedback from other levels. For example, root growth responds favorably to high-N soil, but tree-N status affects this response. Similarly,

stemwood production responds positively to improvement in nitrogen regime, but leaf area display and dynamics may limit this response. Our presentation may be summarized in four considerations.

First, the relationship between nutrients and tree growth is seasonally dynamic. Different parts of the tree grow at different times of the year (e.g., see Figure 12 in Hinckley and Lassoie 1981), so nutrient levels will also change seasonally in different parts of the tree. Within the phenological pattern of a given species, changes in the duration of growth, together with growth rate, will ultimately control allocation. Thus changes in season growth dynamics reflect the way in which the tree allocates carbon under different site and stand conditions.

Second, the magnitude and duration of carbon allocation to foliage, stems, or roots vary according to the availability of nutrients. In temperate forest soils, the nutrient capital is often large but the pool of available nutrients may be small. Thus the seasonal dynamics of nutrient release are another determinant of carbon gain and allocation.

Third, the rates of biological processes control both the availability (microflora, microfauna) and the uptake (root distribution and growth) of nutrients. These processes are linked by the inputs of carbon allocated from aboveground, and are controlled by the effects of soil moisture, and air and soil temperatures, on both plant and microbial processes.

Fourth, evidence exists that carbon and nitrogen are allocated so as to maximize total carbon fixation. This pattern appears to hold from the leaf to the ecosystem level.

Because of the importance of nitrogen and carbon in controlling forest productivity, an evaluation of the impacts of increasing atmospheric CO₂ concentration or of elevated atmospheric nitrogen inputs must consider the carbon and nitrogen relations of tree species over several levels of biological organization.

Some key questions remain: (1) What is the response of total belowground allocation, including root respiration, to altered nutrient regimes? This knowledge is essential, particularly given the tremendous quantities of carbon shunted belowground, to address issues of global change and carbon sequestering. Techniques that quantify net soil carbon dynamics, such as those of Raich and Nadelhoffer (1989), will be an important starting point in this area. However, these techniques need to be evaluated more thoroughly in different ecosystems and at lower levels of biological organization. (2) What are typical whole-tree carbon budgets and how

do they vary with important environmental and management regimes? An example of such data is provided by Linder (1985); however, such budgets need to be estimated from real rather than estimated flux data. (3) What are the environmental, genotypic, and developmental determinants of root and leaf senescence? Given the critical role of these processes in productivity responses of ecosystems, we know very little about them at present.

In the context of nutrient management and research, it is clear that physiological studies must incorporate stand-level processes into the complex of plant and environmental factors studied. Similarly, stand-level manipulations and research must include considerations of how individual trees and tree organs will respond mechanistically to altered environments.

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