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Efficiency of Nutrient Acquisition by Fine Roots and Mycorrhizae

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I. Strategies of Tree Root Systems

As successful dominant plants in many dry and infertile environments, coniferous trees presumably exhibit structural and functional adaptations in the root system that provide a competitive edge when soil resources are in short supply. With this as a precept we advance the general notion that certain properties of the root systems of conifers have evolved to optimize soil resource acquisition under different environmental regimes. Formulating an expression for root system optimality is made difficult by the complex life history of perennials and the multiple functions performed by roots. Moreover, quantitative analysis of the optimal structure or function of root systems has been constrained by the difficulty of root observations and measurements and by the spatial and temporal variation in the soil environment. Nevertheless, recent workers have invoked arguments concerning root foraging strategies to explain variation among root systems of different types of plants or of plants in different environments. For example, root longevity should vary with soil fertility, according to Grime *et al.* (1991):

> Plant strategy theory predicts that mineral nutrition on fertile soils will involve "active foraging" which consists of patch exploitation by morphologically dynamic root systems, in which the life span of individual fine roots is short. On infertile soils it is predicted that root systems will be less dynamic but by remaining functional throughout the year will be capable of intercepting brief mineralization pulses even when these coincide with harsh environmental conditions.

Harper *et al.* (1991) discuss environments that favor strategies of fine-scale branching versus extension growth:

> Water and some nutrients (especially nitrates) can move relatively freely in the wetter soils. Very close proximity of the root surface to the location of the resource is then relatively unimportant and branching at a fine scale will bring little reward. Under these conditions extension growth will tend to be favored over fine-scale branching. . . . If we were to design an ideal root system for growth in a phosphate-limited environment, or for one in which the water status was regularly close to the wilting point, it would have to have a fine-scale and intimate branching pattern and probably have to sacrifice extensive elongation (or develop mycorrhizal association).

Tiffney and Niklas (1985) suggest that rooting density should respond to the patchiness of the environment:

> Root-bearing plants, in contrast to rhizomatous plants, thereby possess both the ability to explore for resources (linear growth) and the ability to exploit resources efficiently when encountered (clumped growth).

In this chapter, we present a quantitative treatment of the strategies of nutrient uptake by tree root systems building on a biophysical model of the soil–root system. The model is used as a tool for synthesizing existing information on conifer fine root dynamics and the soil environment. Recognizing inherent limitations of the information base and the current model formulation, we also consider in qualitative terms some likely implications of crucial root system characteristics such as root diameter, longevity, and mycorrhizal association.

Our principal objectives are to illustrate an approach for improving basic understanding of root system structure and function and to suggest directions for future research on this complex topic. Ultimately, we hope that this approach will be useful both for explaining natural ecological patterns and for guiding forest management.

II. A Model of Fine Root Efficiency

A. Calculating Carbon Expenditure and Nutrient Uptake

A quantitative model of the carbon expenditure and nutrient acquisition of fine root systems makes it possible to explore some of the above-stated claims about the foraging strategies of roots. Specifically, we want to test which of the many variations in root properties across species and environments could be explained as adaptations to optimize the efficiency of nutrient acquisition by roots. Some properties of roots will not be explained by the nutrient-uptake function of roots, such as those required to anchor and support the plant. An analysis parallel to the study of the efficiency of nutrient acquisition could be undertaken to help identify adaptations of roots that improve the efficiency of water ac-

quisition. The present analysis is appropriate to situations in which the availability of nutrients limits plant growth more than does lack of water or support.

An underlying assumption of the present analysis is that plants are energy limited and that there should be an advantage to acquiring nutrients efficiently. Therefore, we define the efficiency of nutrient acquisition by roots as the amount of carbon expended per unit of nutrient taken up, averaged over the lifetime of the root. In simplest terms, then,

$$E = UPTAKE/COST,$$

where E is the efficiency of nutrient acquisition by roots (grams nutrient/gram C expended), *UPTAKE* is nutrient gain (grams nutrient/gram fine root/day), and *COST* is carbon cost (grams C/gram fine root/day), averaged over the lifetime of the root. We do not subtract the nutrient required to construct the root nor do we consider nutrient or carbon resorption on senescence. Current evidence suggests that the amount of retranslocation is small (Nambiar, 1987).

The calculation of carbon cost, *COST*, includes carbon contained in the root and carbon lost in growth respiration and maintenance respiration. These are averaged over the life span of the root to obtain the cost per unit root per day.

$$COST = (C_{root} + Y_g + LY_m)/L,$$

where C_{root} is root C content (grams C/gram root), Y_g is growth respiration (grams C/gram root), Y_m is maintenance respiration (grams C/gram root/day), and L is root longevity (days). This equation could be modified to include other carbon costs such as exudation and mycorrhizae.

The amount of nutrient taken up, *UPTAKE*, depends on properties of the soil as well as those of the root. *UPTAKE* is calculated using the steady-state solution to equations of solute movement to the root surface by diffusion and mass flow and solute uptake at the root surface (Nye and Spiers, 1964). This method uses the average concentration in the soil to calculate the concentration at the root surface (Baldwin *et al.*, 1973; Nye and Tinker, 1977). The rate of uptake is limited at high concentrations by saturation kinetics, rather than being a linear function of concentration (Yanai, 1994). The assumption of a steady-state condition (the rate of solute uptake at the root surface equals the rate of delivery to the root by diffusion and mass flow) means that a single rate of nutrient uptake can be used for a root in a given soil environment. Specifically,

$$UPTAKE = \mathrm{SRL}(2\pi r_0 \alpha C_0 \Delta t),$$

where SRL is specific root length (centimeters/gram root), r_0 is the radius of the root (centimeters), α is the root absorbing power (centimeters/

sec), C_0 is the concentration of substance at the root surface (moles/cm^3); and Δt is the model timestep (seconds); α is calculated from Michaelis–Menton uptake parameters:

$$\alpha = I_{max}/(k_m + C_0),$$

where I_{max} is the maximum rate of uptake (moles/cm^2/sec), and k_m is the concentration at the root surface at half of I_{max} (moles/cm^3). C_0 can be calculated from C_{av}, the average solution concentration, from the following proportion:

$$\frac{C_0}{C_{av}} = v_0\left[\alpha + (v_0 - \alpha)\left(\frac{2}{2-\gamma}\right)\frac{(r_x/r_0)^{2-\gamma} - 1}{(r_x/r_0)^2 - 1}\right]^{-1},$$

where v_0 is the inward radial velocity of water at the root surface (centimeters/sec), r_x is the average radial distance to the next root's zone of influence (centimeters), and $\gamma = r_0 v_0/Db$ (dimensionless), where D is the effective diffusion coefficient (cm^2/sec) and b is the buffer capacity of the soil, or the ratio between exchangeable and dissolved nutrient (dimensionless). These equations are presented by Baldwin *et al.* (1973) and Nye and Tinker (1977) and are derived by Yanai (1994).

The steady-state rate of nutrient uptake provides an estimate of nutrient availability that is appropriate to linking specified environmental conditions to specified root properties. It does not simulate the depletion of the nutrient resource by root uptake. In this model, there is no feedback between exploitation of the soil and the availability of nutrients. Differences in soil fertility are represented by different values of the average concentrations of nutrients in the soil (C_{av}); each value is assumed to apply for the lifetime of the root under consideration. Similarly, roots are represented by a single set of characteristics; we do not consider the distibution of root characteristics in a population of roots of differing morphology, age, and uptake characteristics. Spatial heterogeneity in root density and soil properties is also not considered in this analysis. To be relevant to whole-plant foraging strategies, root properties should be chosen to describe the average root active in nutrient uptake. As a result of this simplification, optimal values of root properties defined by this model apply to the average value rather than to a distribution of values.

B. Parameter Values for Roots

Many of the plant and soil parameters used in our calculations are difficult to measure or estimate. We have used a combination of values appropriate to phosphorus uptake but from different plants and soil types. As a result, the magnitude of individual estimates of carbon costs or nutrient uptake can be highly uncertain. Fortunately, because demonstration of optimal behavior depends on varying those parameter val-

Table I Parameter Values Used in Calculating E

Parameter	Values used in base case calculation	Range of values used in sensitivity analysis	Values for mycorrhizal hyphae
Carbon costs			
C_{root} (g C/g dry mass)	0.48	—	0.48
Y_g (g C/g root)	0.51	0.25 to 4	0.51
Y_m (g C/g root/day)	0.042	—	0.042
L (months)	12	4–40	0.25–3
Uptake, root properties			
r_0 (cm)	0.025	0.01–0.05	0.0003
r_x (cm)	0.4	—	0.044
SRL (m/g root)	20	—	80,000
v_0 (cm/sec)	5.66×10^{-7}	1 E-6–3.0×10^{-6}	1.3×10^{-7}
I_{max} (pmol/cm²/sec)	0.268	0.29–0.066	0.268
k_m (pmol/cm³)	16	—	16
Uptake, soil properties			
C_{av} (μmol/liter)	190	50–190	190
D (cm²/sec)	2.43×10^{-8}	—	2.43×10^{-8}
b (dimensionless)	5.84	—	5.84

ues and observing the effect on nutrient acquisition effeciency, E, it is the directional change in E rather than its quantitative value that is most important. It is possible, however, for the values of one parameter to affect the sensitivity of calculated uptake to another parameter (Yanai, 1994), such as the value of C_{av} determining whether D or I_{max} limits uptake.

The parameters required by the model include those associated with carbon costs of root growth and maintenance, as well as root and soil properties affecting nutrient uptake (Table I). Because uptake is usually calculated on the basis of root dry mass, the carbon concentration of fine roots (C_{root}) is a required parameter, and the standard value of 0.48 g C/g dry mass was used in these calculations (Fahey *et al.*, 1988).

The growth respiration coefficient (Y_g) is difficult to estimate directly (Veen, 1981) and a variety of assumptions about the energetic costs of biochemical synthesis are usually employed to calculate Y_g for roots (Lambers *et al.*, 1983; Johnson, 1990). Considerable uncertainty exists in Y_g values because of limited information on the importance of the alternative respiration pathway (Szaniawski, 1981). The value of Y_g should vary with the biochemistry of root tissues because of differences in the cost of synthesizing different compounds. For example, the cost of lignin synthesis is relatively high because decarboxylation reactions are involved and because part of the substrate is catabolized (Lambers *et al.*, 1983). For our calculations, we used a base case value of Y_g of 0.51 g C/g root, based on measurements of Scotch pine seedlings by Szaniawski

(1981); in other scenarios we varied this value with assumed root chemistry as suggested by Lambers *et al.* (1983) and Johnson (1990).

Maintenance respiration (Y_m) of roots has been estimated for herbaceous (e.g., van der Werf *et al.*, 1988) and woody species (Ledig *et al.*, 1976; Szaniawski, 1981). Szaniawski (1981) estimated Y_m for Scotch pine seedlings growing in solution culture by determining the relationship between total root respiration and root growth rate and extrapolating to zero growth rate. We used this estimate (0.042 g dry mass/g root/day) in the base case scenario, although it should be noted that this value was for seedlings and may be higher than that for roots of older trees.

Schoettle and Fahey (1994) summarized estimates of fine root longevity for *Pinus* species, all of which were calculated from the ratio of mean fine root biomass to annual production. These estimates ranged from a few months to several years; for our base case calculations we employed a value of 12 months.

Diameter distributions of fine roots vary markedly among woody species (Eissenstat, 1992; Fahey, 1992) and between soil horizons (Fahey and Hughes, 1994); few values have been published for coniferous forest trees (Eissenstat, 1992). We used a root radius (r_0) of 0.025 cm (diameter of 0.5 mm), which was less than that measured by Kelly *et al.* (1992) for loblolly pine seedlings, but more than that characteristic of mature northern hardwoods (0.015 to 0.020 cm) (Fahey and Hughes, 1994).

Specific root length, the length per gram of root, is not commonly reported. Fahey and Hughes (1994) measured a SRL of 26.1 m/g for roots less than 1 mm in diameter in mineral soil of mixed northern hardwoods. Roots (<0.5 mm) of red spruce saplings had a SRL of 13 m/g in the mineral soil and 10 m/g in the forest floor (unpublished data). We assumed a SRL of 20 m/g, which is intermediate between these two estimates. A value less than 26 m/g is consistent with the smaller r_0 of our base case (0.025 cm) compared to the length-weighted r_0 of the northern hardwoods of Fahey and Hughes (1994). This value is also in line with an estimate of 21 m/g for slash pine roots <1 mm reported by Eissenstat and Van Rees (1994).

The interroot radial distance (r_x) required in the nutrient uptake calculation is generally calculated from root length density, assuming a uniform distribution of root length in soil (i.e., evenly spaced roots). Kelly *et al.* (1992) report an r_x of 2.0 cm. A much lower value of 0.4 cm was calculated from data of Fahey (1994) for mineral soil roots in a northern hardwood forest, where fine roots had an average SRL of 26.1 m/g and fine root biomass was 220 g/m^2 in the upper 0.3 m of soil. We used this value in our calculations.

The values of v_0, I_{max}, k_m, and C_{av} are those reported by Kelly and Barber (1991) and Kelly *et al.* (1992) for uptake of P by loblolly pine

seedlings growing in pots in modified A horizon soil collected from a fine loamy silicious, mesic Typic Hapludult (Lilly series). The values of D and b differ from those published by Kelly *et al.* (1992) because they have been adjusted to include the solution-phase contribution as recommended by Van Rees *et al.* (1990) (J. M. Kelly, personal communication, 1992).

C. Parameter Values for Hyphae

The parameter values required to calculate the efficiency of mycorrhizal hyphae in nutrient uptake (Table I) were estimated as follows. The C content per gram and the rates of growth respiration and maintenance respiration were unchanged from the values used for fine roots, because the few data available give similar values (P. Rygiewicz, personal communication, 1993; Marshall and Perry, 1987). The carbon required for the formation of fruiting bodies and rhizomorphs not active in nutrient uptake is not included in the model calculation. We used a hyphal diameter of 6 μm, based on a variety of ectomycorrhizal fungi observed in symbiosis and in culture. The length per unit mass was 80,000 m/g, based on a tissue density of 0.44 g (dry weight)/cm^3 (Paul and Clark, 1989). The rate of water uptake, v_0, was calculated from a transpiration rate of 3.3 liters/m^2/day (on a stand area basis) (Knight *et al.*, 1981) and a hyphal mass of 2000 kg/ha, assuming all water uptake was through hyphae. The interroot distance, r_x, was calculated by assuming that the hyphae are evenly distributed in the top 10 cm of soil. We used the I_{max} and k_m for P uptake by roots, because the few measurements of I_{max} and k_m for P uptake by hyphae suggest that the mechanisms and rates of P uptake are similar (Thomson *et al.*, 1990).

These parameter values were selected to characterize ectomycorrhizal fungi. Endomycorrhizae might be expected to be more efficient at carbon and nutrient exchange because of their penetration directly into root cortical cells. Most conifer species in the Northern Hemisphere are largely ectomycorrhizal, but many are also endomycorrhizal (Harley and Smith, 1983). These include genera such as *Cupressus*, *Thuja*, and *Metasequoia*. The genus *Juniperus* has been found to be both ecto- and endomycorrhizal. Gymnosperms from the Southern Hemisphere, including *Podocarpus*, are largely endomycorrhizal.

Little physiological research has been accomplished with endomycorrhizal conifers. Physiological work on endomycorrhizal herbaceous and crop plants suggests that some physiological parameters may be similar to those of ectomycorrhizal plants, whereas others may be vastly different. For example, the range of inflow rates of P into endomycorrhizal white clover roots (1.6 to 46 $\times$ 10^{-15} mol/cm root/sec) (Smith, 1982) was similar to that measured for ectomycorrhizal *Salix* roots (1.4 to 32 $\times$

10^{-15} mol/cm root/sec) (Jones *et al.*, 1991). On the other hand, George *et al.* (1992) found that the hyphae of the endomycorrhizal fungus *Glomus mosseae* were not able to transport substantial amounts of water to the host plant, whereas Duddridge *et al.* (1980) suggested that the rhizomorphs of many ectomycorrhizal fungi have a transport capacity sufficient to permit significant rates of water transport to host trees.

III. Model Limitations

Before the results of our root efficiency calculations can be correctly understood, it is essential that the current limitations of our modeling approach be fully appreciated. Our effort to develop a quantitative theory of tree root system function was stimulated by the frustration of attempts to evaluate objectively arguments about root foraging strategy, such as those quoted in Section I. Caldwell (1979) had suggested that explanations of patterns of root growth and distribution must await such quantification, and our experience with this quantitative approach has revealed some promising avenues for future development. However, several difficulties appear to limit the explanatory power of any quantitative theory of tree root system function. These problems arise from our use of a variant of resource optimization theory (e.g., Bloom *et al.*, 1985) under the assumption that energy availability ultimately limits tree fitness. We discuss the limitations of this approach to quantifying tree root system function in three categories: (1) the complexity of tree life history, (2) optimal versus maximal function of roots, and (3) constraints in model formulation and parameterization. Some of these limitations are specific to our particular treatment whereas others may limit the development of any unifying theory of tree root function.

A. Life History Complexity

Natural selection probably has acted most strongly in that set of environments or stages of plant development in which survival is most tenuous. Thus, our conception of E being maximized for the mature sporophyte may be erroneous. Studies of tree populations indicate that very strong selective filters operate at several stages in life history: seed set, survival, and germination; seedling survival and establishment; and growth to sexual maturity (Harper, 1977). Trees have achieved an elaborate integration of life history characteristics that maximizes the chances of completion of the life cycle in suitable environments, and the design of the tree root system must have been selected toward this goal. In resource allocation terms, this goal has been likened to strategies of minimizing risks (Bloom *et al.*, 1985).

If root system traits that maximize survival at some more critical stage

result in constraints on achieving optimal function at another stage, then apparently suboptimal root system strategies could be retained. For example, Fitter (1989) has suggested that mycorrhizal symbioses may be retained only to achieve maximum nutrient delivery at crucial times, such as the seedling stage and during fruit production. Similarly, intolerant tree species usually become established under conditions of generally high resource availability but potentially high risk from environmental extremes; they undergo severe resource limitations during growth to maturity, and then they persist for decades under conditions of low soil resource availability but high light availability. The optimal root properties in each stage might differ, but the earlier stages must at least partly define the root properties of later stages. In contrast, tolerant species often establish under severe limitation of both energy and soil resources, but must respond to release when both sets of resources are briefly supplied in surplus. Hence, it seems likely that some stages in the tree life cycle operate at suboptimal root efficiency. Perhaps most importantly, for a dominant overstory tree, the assumption of primary limitation by energy availability must be questioned. The availability of carbon should affect the optimal exchange rate between carbon and soil resources, as discussed below.

B. Optimal versus Maximal Root Efficiency

Root foraging strategy can be accurately predicted by an analysis of root efficiency only if root systems have been selected entirely for maximizing nutrient uptake under conditions of energy limitation. However, we know that selection has favored other aspects of root function and that energy is not always limiting to tree fitness. As a result, the maximum value of E may not be optimal for the plant. Whole-plant allocation strategy should be adjusted so that growth limitation is most nearly equal for all resources (Bloom *et al.*, 1985), a situation that may be achieved at less than maximal root efficiency. For example, if nutrients are in short supply while carbon is available in excess, the optimal E for plant growth will be reached at higher nutrient uptake and carbon expenditure than the maximum E. Clearly, the estimation of E is necessary but not sufficient for an economic analysis of allocation strategies. A more sophisticated approach to whole-plant or whole-stand modeling would be required to identify the optimal E for plant growth; our approach can only show the values of root parameters optimal in a given environment for maximizing E.

Departures of root system traits from theoretical predictions of maximum efficiency may provide insights into the trade-offs that are necessary to optimize total root function. For example, despite the undoubted advantage in nutrient uptake efficiency of reducing root diameter, coniferous trees retain relatively coarse root systems (Eissenstat and Van

Rees, 1994). This may be because of limits on design associated with their multiple functions, such as storage, anchorage, and transport.

Another reason why root system strategies might deviate markedly from maximal efficiency is that persistence in the face of temporally varying stresses is more important to tree survival than is maximal growth (Gutschick, 1981). This is true not just as the tree passes through different life stages, as discussed above, but also on a much shorter time scale. Bowen (1985) pointed out that selection for survival under seasonal or less frequent environmental stresses may result in carbon partitioning between roots and shoots that differs from the apparent optimum. In the face of possible climatic change, such an assertion takes on practical importance for plantation forestry.

Because most tree species occupy a wide range of habitats and exhibit only a limited degree of genetic variability and phenotypic plasticity in root system traits, it seems likely that most natural stands operate below both the maximal and the optimal root efficiency. It will be a continuing challenge to practical forestry to further develop the basis for selection of root system traits that improve root uptake efficiency while recognizing that optimal effeciency may differ from maximal efficiency.

C. Constraints of Current Model Formulation

The steady-state approach of our model allows for a straightforward analysis of the costs and benefits of roots with different properties in different environments. Only one calculation is required to characterize the lifetime average rate of nutrient uptake, assuming that properties of both roots and soil are constant for the life of the root or that average values may be used to represent them. Further, because each calculation is made for an individual root, variation in properties of the root system and the soil are ignored. This approach obviously suffers certain limitations; neither root systems nor soils are homogeneous or static.

Most forest soils are patchy; soil resource availability is extremely heterogeneous. Root system traits might be selected as much for efficiently exploiting patchy soil resources as for static exploitation of a homogeneous soil, but optimization of E under such conditions could be complex. For example, species from fertile sites appear to be better at exploiting patchiness because they exhibit higher root growth rates (Grime *et al.*, 1991; Eissenstat and Van Rees, 1994), whereas intraspecific differences in root proliferation within patches may be more closely tied to internal carbon allocation strategies [e.g., for *Pseudotsuga menziesii* (Mirb.) Franco seedlings] (Friend *et al.*, 1990).

Another limitation of our model formulation concerns the use of a single fertility level (nutrient concentration) to describe the soil environment. Although root depletion zones are taken into account, they are assumed to be at steady state; the ability of roots to draw down the nu-

trient content of soil over time is not considered. Reynolds (1975) observed nonsynchronous growth of the feeder roots of *P. menziesii* even when bulk soil conditions seemed to be invariant, and he attributed this pattern to the need for relocation of sites of uptake owing to local nutrient depletion. Reynolds applied the term "tactical organization of the root system" to this nonsynchronous growth, suggesting the probable importance of root tip relocation in defining the maximal or optimal E.

Future exploration of the trade-offs between carbon expenditure and nutrient uptake by roots should take into account both spatial and temporal variation in root systems and the soil environment (Yanai and Eissenstat, 1994). To simulate the local depletion of soil by root uptake would require the model to be implemented over time. The optimal deployment of roots in a patchy environment could also be accommodated with only slight modification to the current model. To address the question of what root strategies optimize plant growth, survival, or reproductive success, as opposed to simply maximizing root E, would require incorporating these notions of carbon costs and nutrient gain by roots with a whole-plant approach to resource values and exchanges.

IV. Root Longevity

A. Model Predictions

1. Root Longevity Our first exploration is of the relationship between root longevity and soil fertility. Grime *et al.* (1991), quoted in Section I, suggested that roots should be long-lived in infertile soil and short-lived in fertile soil. We varied root longevity at different levels of soil fertility to find how optimal longevity (defined as the longevity that gives maximum efficiency) depended on soil fertility.

First, for the case in which nutrient uptake is constant with root age, and hence constant with root longevity (Fig. 1a), average lifetime carbon cost declines with root longevity (Fig. 1b) because the construction cost is spread out over a longer period. The maintenance cost per day is assumed to be constant; at very long life spans, the cost per day approaches the maintenance cost. The effect of carbon cost, therefore, is that long-lived roots are more efficient than short-lived roots (Fig. 1c). Why, then, do plants construct roots that are ephemeral as well as roots that are long-lived? Why does root longevity vary both among species and among roots in different soil environments, even within a single plant (Shoettle and Fahey, 1994)? We will consider how construction cost, nutrient uptake, and water uptake might contribute to differences in the efficiencies of roots of different longevity.

2. Root Longevity and Carbon Cost The construction cost of long-lived roots might be higher than that of short-lived roots, if long-lived roots

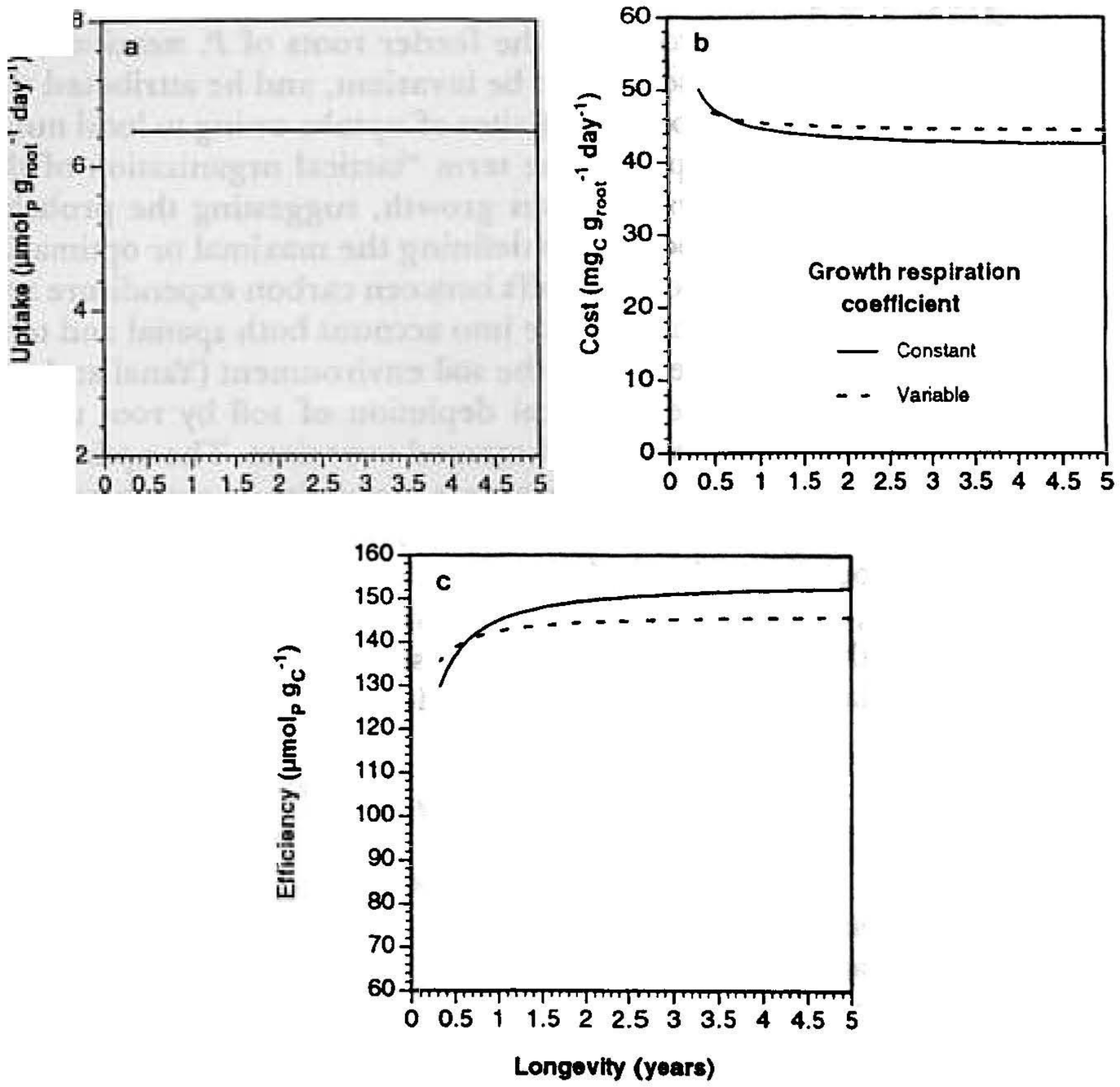

Figure 1 Average lifetime uptake (a), cost (b), and efficiency (c) as a function of root longevity for constant and for varying values of growth respiration. Variation in the growth respiration coefficient was linear with root longevity, ranging from 0.25 g C/g root at a longevity of 4 months to 3.7 g C/g root grown at a longevity of 40 months.

contain higher concentrations of more energetically costly biochemicals, such as lignin and secondary chemicals [Chapin (1989), however, found no basis for this assumption in leaves]. For example, whereas the conversion efficiency of sucrose to cellulose is essentially 1.0, the conversion efficiency of sucrose to lignin is 0.47 (Lambers *et al.*, 1983). When we varied the growth respiration of roots as a function of longevity (Fig. 1b), we found that even a very steep relationship of growth respiration to longevity did not make cost increase at high longevity, because the tendency of increasing longevity to reduce cost was so strong. Variation in construction cost, therefore, fails to indicate an optimal longevity. Further, an optimal longevity derived by this means would not be sensitive to soil fertility.

3. Root Longevity and Nutrient Uptake Another possibility to consider in explaining the advantage of root turnover is that short-lived roots are more effective at nutrient uptake than are older roots. Although it seems likely that uptake rates vary with root age, largely as a result of progressive suberization and mycorrhiza formation (e.g., Queen, 1967; Chung and Kramer, 1975), the magnitude and shape of this relationship are unknown. To explore this mechanism, we assumed a linear relationship between longevity and I_{max}, the saturation constant for uptake at the root surface. The resultant relationship between uptake and longevity is nearly linear at high soil fertility, with uptake highest in the most ephemeral roots (Fig. 2a). In an infertile soil, there is less advantage to roots of

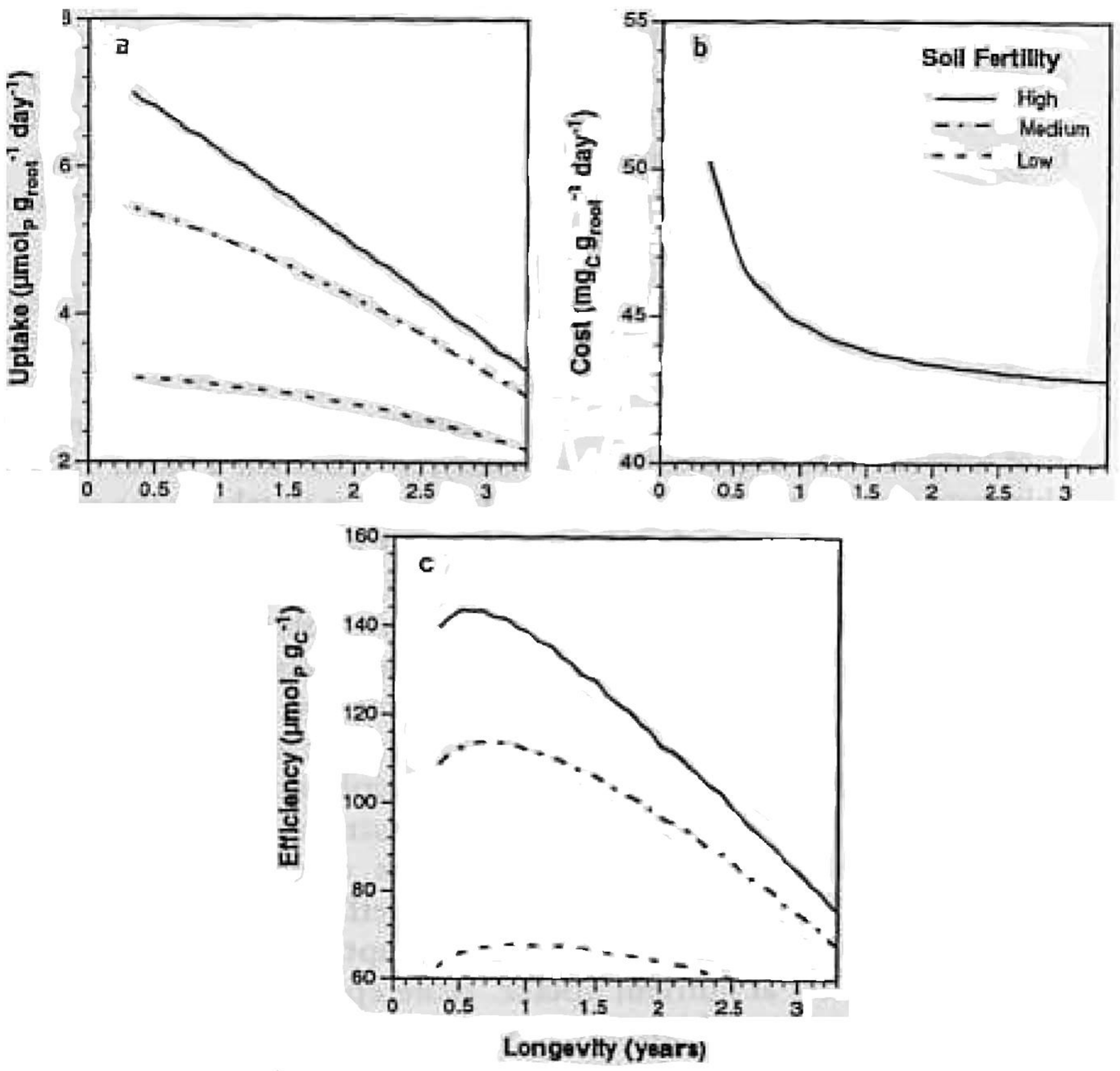

Figure 2 Average lifetime uptake (a), cost (b), and efficiency (c) as a function of root longevity, with nutrient uptake varying with root longevity. Maximum P influx rate (I_{max}) declined linearly from 0.29 pmol/cm²/sec at a longevity of 4 months to 0.13 pmol/cm²/sec at a longevity of 40 months. Soil of high, medium, and low fertility had P concentrations of 190, 100, and 50 μmol P/liter.

very high uptake capacity, because modeled nutrient uptake is limited by the rate of solute movement to the root surface, not by the kinetics of uptake by the root. As a result, short-lived roots in infertile soil absorb less nutrient than the same roots in more fertile soil. Long-lived roots, in contrast, are limited by the kinetics of nutrient uptake in our example, and uptake by long-lived roots is similarly low in fertile and infertile soil. This result follows from our assumption that an average I_{max} characterizes the root throughout its life. If the calculation were made with I_{max} declining as the root aged, the advantage of fertile soil to young roots would contribute to the average uptake by long-lived roots.

The effect of carbon cost (Fig. 2b) is to make ephemeral roots inefficient; the effect of low nutrient uptake rates at high longevity tends to make long-lived roots inefficient as well (Fig. 2c). The optimal longevity depends on the combination of values of the other parameters in the model. In our example, the optimal longevity in fertile soil is about 6 months, with the optimal longevity in infertile soil about 1 year. Of course, roots in infertile soil are less efficient than roots in more fertile soil, in terms of carbon expended to obtain a unit of nutrient.

4. Root Longevity and Water Uptake Water uptake rates affect solute uptake, especially when uptake is limited by the rate of delivery of solute to the root surface (Yanai, 1994). Changes in the rate of water uptake with root longevity might provide an alternate explanation of optimal root longevity. To explore this possibility, we assumed a linear relationship between longevity and the velocity of water uptake at the root surface (v_0). There is some justification for this assumption; for example, Sands *et al.* (1982) observed that water uptake rates were about half as high for suberized as for nonsuberized roots of loblolly pine. The effect of declining water uptake rates with root age was to reduce nutrient uptake at high longevity (Fig. 3a). In infertile soil, nutrient uptake increases almost linearly with increasing v_0. In more fertile soil, the advantage of short-lived roots with high v_0 is diminished; nutrient uptake is limited by I_{max}, the saturation constant for nutrient uptake.

Assuming a constant growth respiration coefficient and constant maintenance respiration costs (Fig. 3b), the effect on efficiency of making long-lived roots more resistant to water uptake was similar to that of making them slow at nutrient uptake. More ephemeral roots were inefficient because of their high carbon cost, whereas more long-lived roots were inefficient because of their low nutrient uptake. However, the effect of soil fertility on optimal longevity in the case of varying v_0 was the opposite of the case of varying I_{max}. Optimal root longevity for maximizing the efficiency of nutrient uptake in the fertile soil was quite broad,

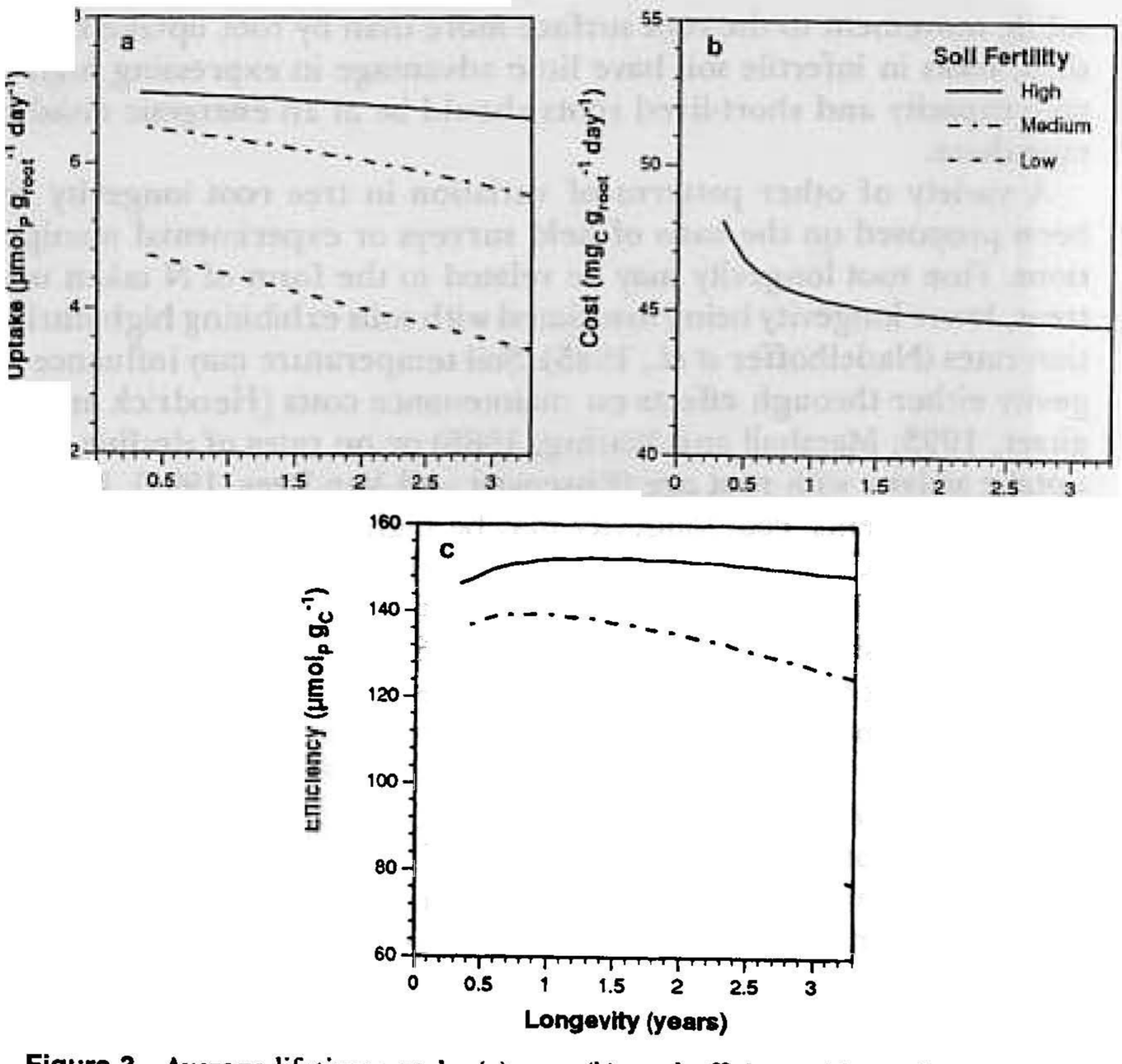

Figure 3 Average lifetime uptake (a), cost (b), and efficiency (c) as a function of root longevity, with water uptake varying with root longevity. The radial velocity of water uptake at the root surface (v_0) was assumed to vary linearly with longevity from 3×10^{-5} cm/sec at 4 months to 51.1×10^{-5} cm/sec at 40 months. Soil of high, medium, and low fertility had P concentrations of 190, 100, and 50 μmol P/liter.

between 1 and 2.5 years. Optimal longevity decreased with decreasing soil fertility, because of the higher advantage given by high v_0 at low fertility.

B. Discussion

Previous theoretical arguments (Grime *et al.*, 1991), as well as limited empirical evidence (Nadelhoffer *et al.*, 1985, Schoettle and Fahey, 1994), suggest that tree root longevity is higher on infertile soils than on fertile soils. Similarly, our model suggests that if I_{max} declines with increasing longevity, the maximum efficiency of root uptake is exhibited at values of longevity that increase with decreasing fertility. This pattern results from model predictions that nutrient uptake in infertile soil is limited by

solute movement to the root surface more than by root uptake kinetics; thus, roots in infertile soil have little advantage in expressing high uptake capacity and short-lived roots should be at an energetic disadvantage there.

A variety of other patterns of variation in tree root longevity have been proposed on the basis of field surveys or experimental manipulations. Fine root longevity may be related to the form of N taken up by trees, lower longevity being associated with soils exhibiting high nitrification rates (Nadelhoffer *et al.*, 1985). Soil temperature may influence longevity either through effects on maintenance costs (Hendrick and Pregitzer, 1993; Marshall and Waring, 1985) or on rates of decline in root uptake activity with root age (Eissenstat and Van Rees, 1994). In patchy soil environments, root longevity may be higher in fertile than in infertile microsites (Pregitzer *et al.*, 1993; Fahey and Hughes, 1994), contrary to model predictions for uniform soil. Finally, thinning of conifers on nutrient-rich sites reduces root longevity (Santantonio and Santantonio, 1987). Each of these patterns of root longevity is discussed below.

The extra energy cost of NO_3 uptake is associated mostly with the high cost of NO_3 reduction; the theoretical Y_g value of protein synthesis from NH_4 is 0.84 whereas for NO_3 it is 0.58 (Johnson, 1990). Although this difference depends on the proportion of NO_3 reduction occurring in foliage, current evidence suggests that for most coniferous forest trees this proportion is probably very low (Andrews, 1986). We incorporated the influence of the differing energy costs of NH_4 versus NO_3 uptake on the longevity associated with maximum root efficiency, with inconclusive results. Not surprisingly, efficiency declined markedly as the proportion of NO_3 absorbed increased from 0 to 1. However, the longevity at maximum efficiency did not change appreciably across this gradient. The longevity at maximum root efficiency was not sensitive to the form of N absorbed because the cost differences were not stongly dependent on longevity. Nadelhoffer *et al.* (1985) observed root longevity differences between nitrifying and nonnitrifying soils that may be explained in part by root uptake costs, but it is uncertain whether these differences would tend to maximize uptake efficiency. Many questions about nitrogen economy and root function that could influence such considerations remain unanswered: What are the differences in costs associated with ion leakage (Johnson, 1990)? What proportion of nitrate reduction and amino acid synthesis actually occurs in the roots (Gutschick, 1981)? What is the energy cost of protein turnover, especially for nitrate reductase (Amthor, 1984)?

Root longevity could be sensitive to soil temperature because of the lower maintenance respiration costs at lower temperatures (Ryan, 1991).

Hendrick and Pregitzer (1993) observed a slight increase in root longevity of sugar maple-dominated forests along a gradient of decreasing soil temperature, in agreement with some of the experimental results of Marshall and Waring (1985). Model calculations show a shift in optimal longevity to shorter life spans with increasing temperature, assuming I_{max} decreases with longevity (R. D. Yanai and D. M. Eissenstat, unpublished data, 1994). Again, the question of whether root longevity is actually optimized across a soil temperature gradient awaits further research, as does the important practical question of whether such variation reflects phenotypic plasticity or ecoclinal, genetic variation as has been observed for a variety of other temperature-regulated traits of trees (Muona, 1990).

The role of patchiness in soil fertility in regulating root longevity adds further complexity to the optimization of root longevity. Although fine root longevity appears to be lower in fertile than in infertile soils, two recent studies in northern hardwood forests have documented higher longevity of roots in fertilized microsites than in adjacent unfertilized areas (Pregitzer *et al.*, 1993; Fahey and Hughes, 1994). Both studies also showed about a sixfold increase in root growth within fertilized microsites. These results further suggest extending our modeling approach to incorporate spatial variation in soil resource availability and the depletion of soil by root uptake. The root proliferation and higher longevity observed in fertile microsites probably could be explained as a whole-root system strategy to maximize uptake efficiency, and might result mechanistically from the absence of depletion zones or from the relatively high overall nutrient transport along mother root axes that penetrate fertile microsites (Fahey and Hughes, 1994).

Changes in canopy structure could influence root longevity. For example, observed effects of overstory thinning on root longevity might be connected with respiratory costs: decreased longevity of *Pinus radiata* fine roots on fertile sites in New Zealand (Santantonio and Santantonio, 1987) might be associated with increased soil temperatures. However, many other influences could be postulated, including changes in carbon allocation.

Finally, it should be noted that the mechanisms of root mortality are poorly understood (Schoettle and Fahey, 1994), and the importance of internal cues for root sloughing compared with external causes, such as drought, anoxia, and herbivory, has not been resolved. For example, recent evidence suggests the possible importance of soil fauna in root mortality (Atkinson, 1992). If external effects that are largely outside the control of the tree play a major role in root turnover, then the notions of optimality developed here must be modified to reflect these effects.

V. Root Diameter

A. Model Predictions

We were unsuccessful in our attempts to establish an optimal diameter of roots for maximum nutrient uptake efficiency. The model indicates that uptake per gram of root increases indefinitely as roots get finer (Fig. 4a). This is because root length and root surface area per unit mass of root increase as diameter decreases. If the carbon cost per unit mass of root were constant, the optimal root for nutrient absorption would be infinitely fine (Fig. 4c). Other factors, such as structural constraints, presumably limit the diameter of fine roots. This illustration supports the long-held view that the efficiency of mycorrhizal hyphae is due to their having smaller diameters than are possible for roots.

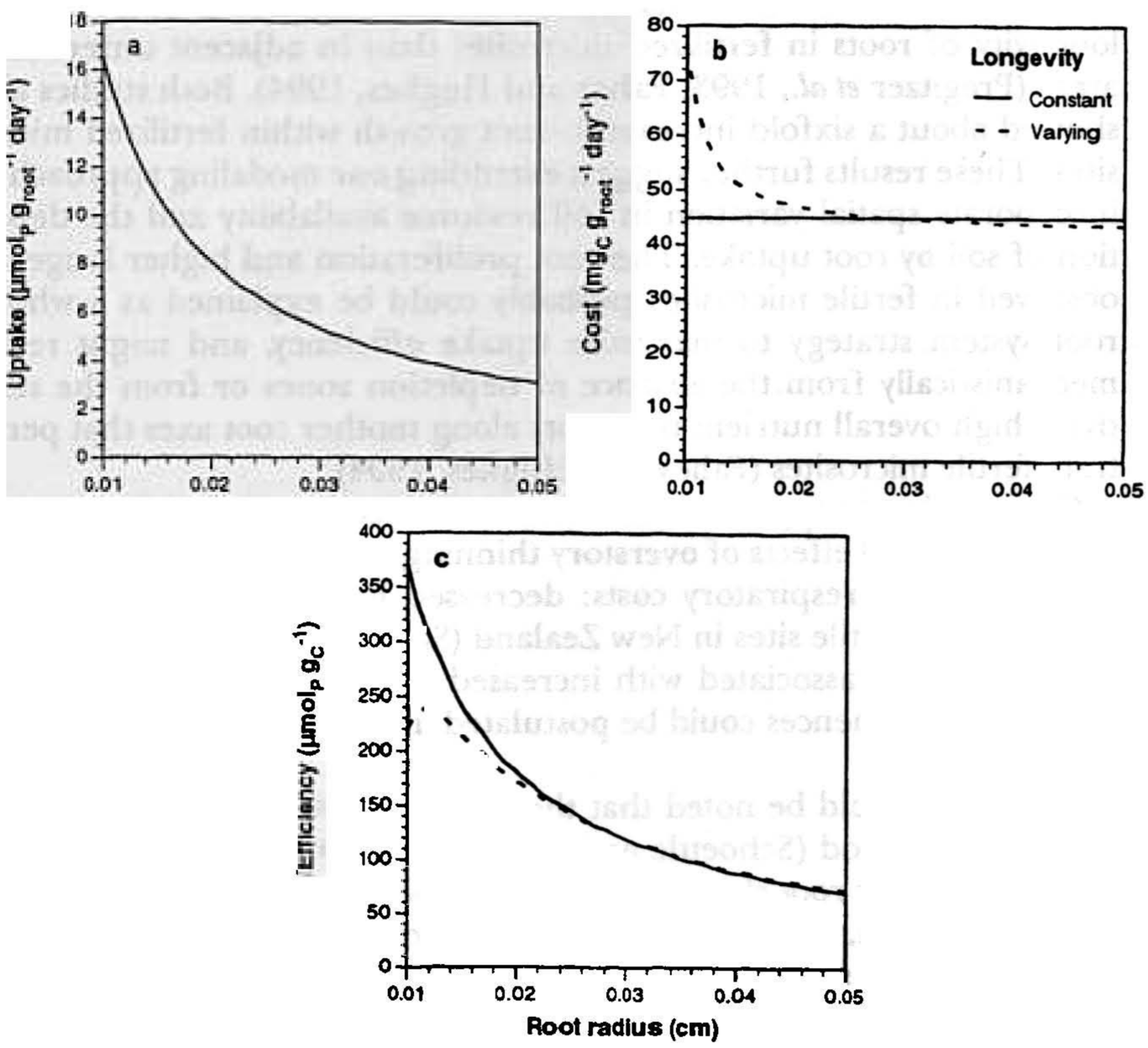

Figure 4 Average lifetime uptake (a), cost (b), and efficiency (c) as a function of root radius (r_0), assuming either constant longevity or longevity varying with root diameter, from 1 month at r_0 = 0.01 cm to 24 months at r_0 = 0.05 cm.

We explored whether a higher carbon cost associated with finer roots could increase optimal root diameter. A shorter life span associated with finer roots would produce such a carbon cost. Assuming a relationship between diameter and longevity creates a curve of C cost with diameter (Fig. 4b) that looks like that of C cost with longevity (Fig. 1b). The resulting curve does have a maximum efficiency and optimal diameter (Fig. 4c); the value of this optimal diameter is a reflection of the relationship we assumed with root longevity, not a quantitatively supported prediction.

B. Discussion

The results of our simulations indicated that, unless root longevity is strongly tied to root diameter, average lifetime root efficiency increases continuously with decreasing diameter. Most likely, other root functions or anatomical constraints limit the minimum diameter of roots. For example, larger diameter roots may be able to withstand greater soil impedence before buckling (Whitely *et al.*, 1982). The root cortex may serve as a short-term reservoir for nutrient storage. Glass and Siddiqi (1984) observed that under K limitation, shoot K remained constant while root concentration declined markedly, indicating that K stored in the root cortex had been transported to maintain shoot K concentrations. In pines, only diarch and tetrarch roots (i.e., those of relatively large diameter) appear to be morphogenetically capable of becoming mother roots (Wilcox, 1968), and hence of long-distance, exploratory growth, illustrating a trade-off necessitated by existing root system design. The mycorrhizal symbiosis provides absorbing surfaces of much smaller diameters than roots, with consequent advantages, as we have illustrated. In addition, root hairs might be considered a plant adaptation in the direction of finer absorbing organs. The effect of root hairs on nutrient uptake can be simulated by increasing the effective radius of the root by the average length of the root hairs; it would be misleading to consider them independently of the roots because root hairs, to a greater extent than hyphae, operate within the depletion zone of roots. Alternatively, the principal role of root hairs might be to prevent the development of root–soil gaps and the resulting resistance to solute transport to the root surface (Caldwell, 1979), rather than to enhance the absorbing area of roots. To the degree that the formation of root–soil gaps increases with root age, this factor is represented in our analysis of root uptake rate decreasing with longevity, and would contribute to the benefits of rapid root replacement. If large-diameter roots are more likely to suffer root–soil gaps, then the advantages of small-diameter roots in nutrient uptake would include the benefit of more continuous nutrient uptake.

VI. Efficiency of Mycorrhizal Hyphae

A. Model Predictions

Mycorrhizal associations are common in conifers (Miller, 1982) and are known to be beneficial in cases of nutrient scarcity, particularly of N and P. Absorption rates of N and P, reported on the basis of root mass or root length, are increased by mycorrhizal infection of plants at low fertility (e.g., Smith, 1982). A partial explanation for this increased nutrient uptake ability can be found by comparing the uptake and efficiency of roots and mycorrhizal hyphae. If the C cost per unit mass of absorbing tissue (root or hypha) and the P uptake kinetics are assumed to be the same for roots and hyphae (Table I), then the efficiency of hyphae is orders of magnitude greater than the efficiency of roots (Table II), due to the increase in length of the absorbing organ per unit mass, as predicted from the previous exploration of variation in root diameter. Differences in the uptake rates of roots and hyphae may also be important, although few measurements for extramatrical hyphae and ectomycorrhizal roots are available and none appears appropriate to our modeling approach (Miller and Allen, 1992; Finlay, 1992). Mycorrhizae may also increase P uptake by increasing P in solution (Harley and Smith, 1983; Bowen, 1973); this effect is not included in the model. The efficiency of the mycorrhizal association, calculated using the cost of roots plus hyphae and assuming that uptake is achieved through the hyphae (Table II), is intermediate between that of the hyphae alone

Table II Uptake, Cost, and Efficiency of Roots and Hyphae[a]

Fertility (μmol P/liter)	Root	Hypha	Root + hyphae
	Uptake (μmol P/day)		
190	6.7	323	165
100	6.3	302	154
50	5.4	264	134
	Cost (g C/day)		
All	0.045	0.075	0.060
	Efficiency (μmol P/g C)		
190	150	4310	2760
100	140	4010	2570
50	122	3520	2250

[a]The combined effect of roots and hyphae assumes equal amounts of each. Hyphae were assumed to turn over monthly, roots annually. All other parameter values are shown in Table I.

(which does not include the support of the root system) and the roots alone (which includes neither the cost nor the benefit of association with the fungus). A more complete evaluation would include the effects of mycorrhizal association on root longevity and respiration; these refinements, however, are unlikely to change the result that, from the point of view of the efficiency of carbon expenditure for nutrient gain, it would seem advantageous to expend carbon for mycorrhizal development rather than for roots wherever possible.

Although conifer species are universally mycorrhizal (Meyer, 1973), ectomycorrhizae generally are more fully developed on infertile than on fertile soils or where nutrients become available in seasonal flushes (Högberg, 1986; Harley and Smith, 1983). We tested the hypothesis that differences in mycorrhizal development in these different environments could be explained by differential efficiency. We found, however, that hyphae are much more efficient than roots at P uptake regardless of the soil concentrations of P (Table II), which is not consistent with experimental results (Rousseau and Reid, 1990). The lack of mycorrhizal development on fertile soils, therefore, is most likely due to other factors (discussed below).

Turnover rates of ectomycorrhizal hyphae remain largely unquantified in the field. Although Fogel and Hunt (1983) were able to calculate the overall monthly changes in the standing crop of soil and litter hyphae for a coniferous forest site in Oregon, it was not possible to follow the fate of any given cohort of hyphae. Because of the rapid growth rate and relatively small size of fungal hyphae compared to roots, turnover rates are undoubtedly much more rapid for fungal hyphae than for roots. We explored whether the short life span of mycorrhizal hyphae could be explained by consideration of the efficiency of uptake. As in the case of roots (Fig. 1), if uptake is assumed to be constant with hyphal longevity, then efficiency only increases with longevity, due to the amortization of construction costs. We assumed a rapid decrease of I_{max} with hyphal age, resulting in a decrease of uptake with longevity (Fig. 5). The resulting longevity to maximize E is much less than for roots because of the rate at which we assumed uptake to decline with hyphal age. Optimal longevity did not vary, in this case, with soil fertility.

B. Discussion

The extraordinary efficiency of mycorrhizal hyphae compared to roots should make it advantageous, in terms of C conservation, for any plant to use hyphae rather than roots for nutrient uptake. We need look no further to explain why coniferous forests have obligate relationships with ectomycorrhizal fungi; the mystery, perhaps, is why some plants have less mycorrhizal development than others. Specifically, why is it that

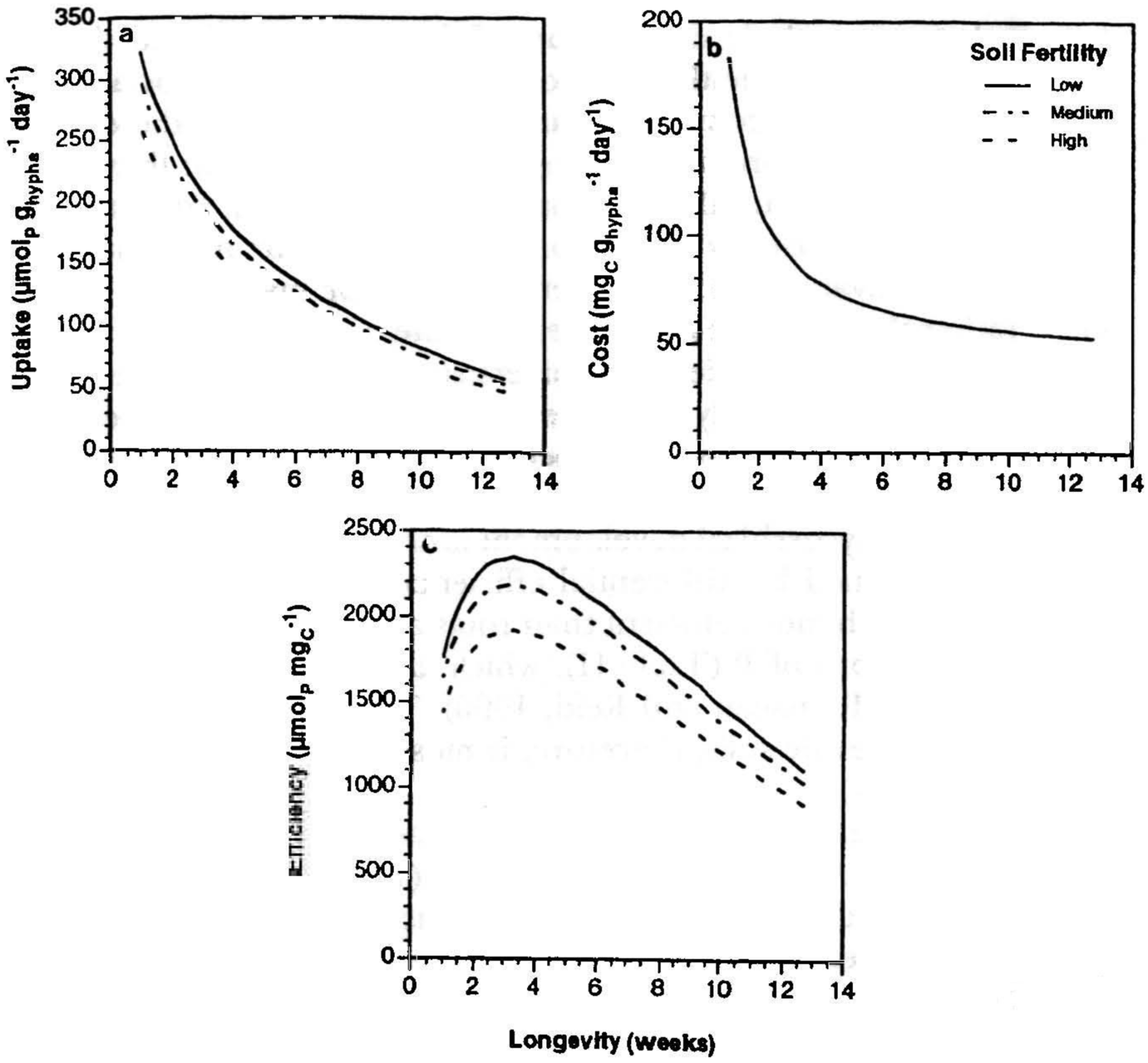

Figure 5 Average lifetime uptake (a), cost (b), and efficiency (c) of mycorrhizal hyphae at three levels of soil fertility, assuming I_{max} declined from 0.27 pmol/cm²/sec at a longevity of 1 week to 0.05 pmol/cm²/sec at a longevity of 13 weeks. Soil of high, medium, and low fertility had P concentrations of 190, 100, and 50 μmol P/liter.

trees are more likely to develop ectomycorrhizae in poor soils? There are possible causes of variation other than differences in carbon and nutrient availability.

Hemlock (*Tsuga*) species thrive in wet and nutrient-rich soils, often surviving for a year or more before developing mycorrizae (Kropp, 1982). Fewer species of fungi may inhabit these soils (*Elaphomyces granulatus* being one notable exception). Anaerobiosis, high nitrogen availability, and acid soil may contribute to the scarcity of ectomycorrhizae in these conditions. To the degree that nutrient-rich soils tend to develop in more favorable environments—with higher organic matter contents, higher water-holding capacity, and lower pH—soil characteristics other than nutrient supply may contribute to the variation in fungal availability across habitats (Harley and Lewis, 1969). Nutrient supply, however,

also appears to have a direct effect: laboratory studies have shown that high levels of N fertilization decreased ectomycorrhizal formation (Hacskaylo and Snow, 1959).

Variations in the relative importance of nutrient acquisition and carbon conservation may also help explain variation in mycorrhizal formation across habitats. First, plants with little or no mycorrhizal development might be unlikely to survive in an infertile soil but might be at much less of a disadvantage in nutrient-rich soil. In other words, the higher value of nutrients in the nutrient-poor condition increases the value of the benefit obtained for carbon investment belowground. The value of carbon, too, varies with the plant environment. In the nutrient-poor condition, where growth is limited by nutrient availability, carbon is available for investment in mycorrhizal fungi with few competing sinks elsewhere in the plant. In contrast, where nutrients are plentiful, plant growth may be limited by carbon availability, and the expense of allocating carbon belowground is greater. In short, the relative value of C and nutrient in the accounting system of the whole plant will vary with environmental conditions, affecting the optimal efficiency of carbon–nutrient exchange, as discussed in Section III,B.

One limitation to nutrient supply to plants via mycorrhizae is the transport of nutrient from fungal tissues to root tissues. If the rate of nutrient absorption by the root is still limited by its own uptake kinetics (Smith and Smith, 1990; Cairney and Smith, 1992), then increases of orders of magnitude, as shown in Table II, are unlikely to be realized. The rate of transport along the hyphae may also limit the transfer of nutrients to the plant. Neither of these factors has been considered in this analysis.

Another factor that has generally been ignored but that may be very important is the effect of ectomycorrhizal fungi on the availability of soil resources. For example, ectomycorrhizal fungi have now been shown to take up N from complex organic molecules (Abuzinadah and Read, 1986a,b; Abuzinadah *et al.*, 1986; Dighton *et al.*, 1987; Finlay *et al.*, 1992); much of this N becomes directly available to the plant. Because there is far more organic N than mineralized N in soils from coniferous forests, our conception of N availability to plants (that only mineralized N is taken up) may require substantial revision.

The supply of carbon to mycorrhizae through this saprotrophic activity has also been previously unrecognized. Finlay *et al.* (1988, 1989) found that ^{15}N-labeled organic N is taken up primarily as amino acids by ectomycorrhizal fungal mycelia. These amino acids can either be transported to the mycorrhizas or stripped of their N and the carbon skeletons utilized by the fungus for a variety of physiological processes (Finlay, 1992). Finlay (1992) further suggests that amino acids derived from the incorporation of ammonium into carbon skeletons from fungal

sugars are released to the plant root, providing a route for the reverse translocation of carbon from fungus to host.

In the present context, it may be helpful to view the energy required to acquire N from organic sources by ectomycorrhizal fungi as a belowground ecological pyramid. Because ectomycorrhizal fungi are able to cycle N (originating as discarded material from the host primary producer) directly back to the host (also the primary consumer), the classical N mineralization cycle is circumvented. More N is therefore available to the host with much less immobilization and much less total energy loss than if the same organic N were completely mineralized before it became available again.

The study of plant ecophysiology and the study of mycorrhizal fungi have long been independent, to the detriment of both. The importance of mycorrhizae in carbon budgets (the biomass of extramatrical hyphae can be considerable) and nutrient uptake is often ignored. Because the uptake parameters I_{max} and k_m might be different for fungi than for roots, calculating root uptake based on uptake parameters measured for roots alone could be misleading. More research in the area of mycorrhizal contributions to tree function is clearly warranted.

VII. Summary

It is difficult to assess claims about the adaptive advantages of root foraging strategies without a conceptual model specific enough to allow quantitative prediction and testing. Application of a solute uptake model in combination with a calculation of carbon costs provides a means of assessing the efficiency of carbon expenditures in procuring nutrients from soil. Although many of the parameters required to calculate root efficiency are poorly known at present, such that costs and benefits cannot be accurately quantified, the model can be used to test hypotheses for internal consistency and for correspondence to observed patterns of root growth in different soil environments.

We analyzed the optimal values of root properties, such as longevity, diameter, and mycorrhizal association, that maximized the efficiency of carbon exchange for nutrient uptake in different environments. Optimal longevity was found to decrease with increased soil fertility if the kinetics of nutrient uptake were assumed to decline with increased root longevity. Optimal diameter was found to be smaller than observed in roots, suggesting that other constraints on root structure or function limit their minimum diameter. Mycorrhizal hyphae were found to be more efficient than roots regardless of soil fertility.

The steady-state approach to calculating carbon costs and nutrient

gain enabled combinations of root and soil properties to be very simply evaluated. However, this approach ignored spatial heterogeneity and temporal variation in root and soil properties, such as aging of roots and patchiness of soil fertility. Furthermore, finding the values of root parameters that maximize root E may not predict the optimal root deployment for the plant, which depends on the relative value of carbon and nutrients in the whole plant. Estimation of the rate of exchange of carbon and nutrients in roots is a necessary step toward an economic analysis of allocation strategies; it also reveals areas of ignorance and helps to identify future research needs.

Acknowledgments

We are grateful to Dave Eissenstat and Tom Hinckley for review of the manuscript and to Gail Blake and Carol Zollweg for technical support. Financial support was provided to TJF by National Science Foundation Grant BSR-87002331, to SLM by National Science Foundation Grant BSR-8805983 and United States Department of Agriculture Grant 91-37101-6759, and to RDY by the Boyce Thompson Institute for Plant Research, the Electric Power Research Institute under research contract number RP2799-1, and the USDA Forest Service, Southeastern Forest Experiment Station (Southern Global Change Program), through contract TV-8644OV with the Tennessee Valley Authority. The Southern Global Change Program, a coordinated effort of the Southeastern and Southern Forest Experiment Stations, is one component of the Forest Service's Global Change Program. This paper has not been subjected to Forest Service policy review and should not be construed to represent the policies of the agency.

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