Mycorrhiza (1992) 1:83-89

Mycorrhiza

Mycorrhizae and forest ecosystems

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Summary. Mycorrhizae play an important role in regulating patterns of energy and nutrient flux in terrestrial ecosystems. To conceptualize this role I develop the theory behind a simple index of the efficiency of soil resource acquisition by plant root systems (E). The morphological, physiological and demographic characteristics of mycorrhizae that define E appear to vary with environment and with plant community composition. This theory is elaborated with examples drawn from forest ecology literature. Some inconsistencies among observations of fine root dynamics are particularly revealing: (1) belowground carbon allocation vs soil fertility; (2) causes of root mortality; (3) root longevity vs decomposition rates. A comprehensive theory of mycorrhizal and ecosystem dynamics must await resolution of these inconsistencies and better quantitative information on mycorrhizal features affecting E.

Key words: Fine roots - Physiology - Morphology - Demography

Introduction

Patterns of energy and nutrient fluxes in the biosphere often transcend the patterns of community distribution and species abundance. Ecosystem research seeks to explain the former patterns, particularly with regard to the intensity of fluxes and the relationships among fluxes of energy and various critical materials such as water and plant nutrients. For example, one of the first major ecosystem paradigms grew from the observations of Waksman (1932) that net mineralization of nitrogen from plant debris is restricted until a critical C:N ratio is reached in the substrate. Redfield (1958) extended this principle by demonstrating how the marine biota regulate the chemical composition of the world's oceans (p. 206):

> "The synthesis of organic matter is a highly selective process which results in products having specific composition. ... In the decomposition of a given amount of organic matter the quantity of oxygen consumed must be determined exactly by the quantities of carbon, nitrogen, etc., to be oxidized, and the relative changes in the quantity of oxygen, phosphate, nitrate, and carbonate in the water must depend exactly on the elementary composition of the plankton."

Thus, a mechanistic basis for understanding nutrient behavior in the biosphere has followed from the recognition that element ratios in the tissues of dominant organisms regulate nutrient recycling in ecosystems (Vitousek et al. 1987).

Because the patterns of energy and material fluxes constrain the distribution of species and partly define the sets of traits of those organisms that are successful competitors in any particular site, then to the extent that these patterns transcend community composition, they may be regarded as primary regulators of the organization and arrangement of the biosphere. However, the biota exert a profound influence over energy and material flux so that the relationships between ecosystem level patterns of flux and community patterns of species composition have evolved with the biota and its distribution. Mycorrhizae are a crucial feature in this connection.

In this paper I will attempt to provide a conceptual framework for improving understanding of the role of mycorrhizae in energy and nutrient fluxes in the biosphere. Although some contributions to such a framework have been made (e.g., Heal and Dighton 1985), the relative scarcity of quantitative information apparently has limited such efforts. My approach will be to construct a theory of mycorrhizal dynamics in relation to energy and nutrients, based upon the efficiency of soil resource acquisition by plants. In light of this theory, some recent observations of mycorrhizal activity in temperate forests will be used to illustrate the nature of existing uncertainties and to point towards fertile lines of inquiry. I hope that these observations will stimulate mycorrhizae experts to continue to explore the connections between ecosystem organization and the dynamics of their fascinating symbiosis.

Efficiency of soil resource acquisition

A central concept in a unifying theory of mycorrhizal dynamics is the efficiency of soil resource acquisition by plants. This efficiency (E) can be defined as the mass of limiting nutrient absorbed per unit fixed energy (carbon) allocated to roots for growth and maintenance. The value of E for the entire root system of an individual plant represents the average of that for each individual root. Various morphological, physiological and demographic characteristics of fine roots and mycorrhizae interact with environmental constraints to define the value of E for any individual root over its lifespan and of the entire root system of a plant over its lifespan. A finely tuned feedback between energy (carbon) and nutrient status of the whole plant and the efficiency of and allocation to roots and mycorrhizae is surmised (Fig. 1). The outcome of competitive interactions between individuals and populations in natural communities should reflect differences in this overall efficiency under the set of environmental constraints encountered in any particular ecological situation.

Because the constraints on maximizing E should vary markedly along broad environmental gradients, a paradigm for mycorrhizae and ecosystem dynamics could be framed within the context of quantitative models describing the components affecting E and thereby defining the patterns of mycorrhizal activity in energy and nutrient flux processes. I will group these components into four categories: (1) morphological characteristics; (2) physiological characteristics; (3) root longevity; and (4) environmental characteristics.

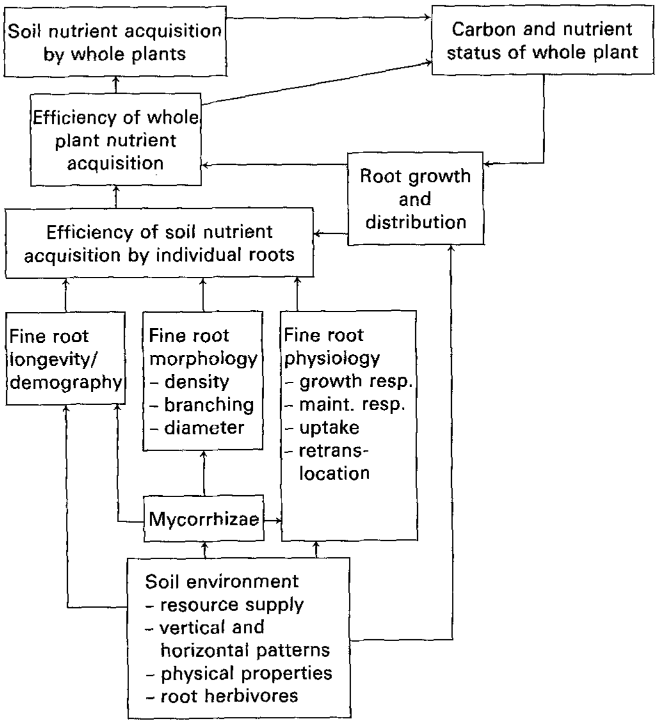

Fig. 1. Conceptual model of the feedbacks and interactions between plant nutrient acquisition, carbon allocation, and root and soil component affecting the efficiency of soil nutrient acquisition

Morphological characteristics

Assuming equal rates of nutrient uptake and respiration per unit root length or surface area, roots of smaller diameter and lower tissue density will be more efficient in nutrient acquisition than larger or denser roots. Thus, the diameter distribution, specific root length (i.e., mass per unit length) and branching patterns (i.e., number of root tips per unit length) of the fine root systems probably have important effects on the efficiency of resource acquisition as demonstrated by Robinson (1986). Each of these features may vary both among species and spatially within heterogeneous

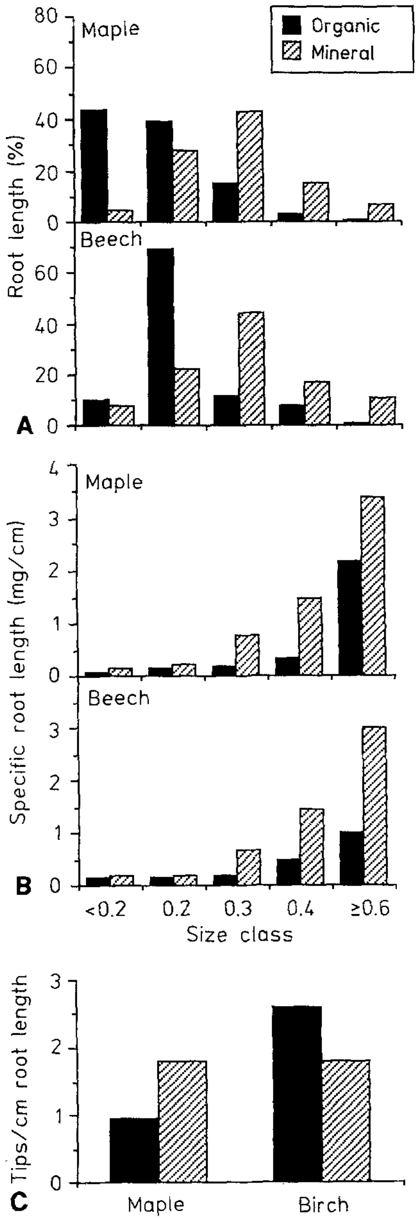

Fig. 2A–C. Variation in fine root morphology between organic and mineral soil horizons for dominant trees (sugar maple, American beech, yellow birch) at Hubbard Brook Experimental Forest, N.H. **A** Size-class distributions, **B** specific root length, **C** root branching soil environments (Ford and Deans 1977). For example, in a northern hardwood forest at Hubbard Brook Experimental Forest (HBEF), New Hampshire, the size-class distributions, specific root length, and branching patterns of fine roots varied among species and between organic and mineral soil horizons (Fig. 2). As discussed later, the ubiquitous extramatrical hyphae of mycorrhizal fungi eventually must be included as a component of root system morphology.

Another morphological feature affecting the efficiency of the plant root system as a whole is the plasticity of morphological characteristics in the face of spatial or temporal heterogeneity in resource availability. Sibly and Grime (1986) described the theoretical basis for optimal strategies of soil resource acquisition that depend upon the degree of environmental heterogeneity. Crick and Grime (1987) provided experimental evidence for two contrasting strategies for maximizing E under differing conditions of nutrient availability: a dynamic (rapid turnover, high maximum rate of uptake) and morphologically plastic root system is advantageous under fertile, competitive situations, whereas a large, unresponsive system is favorable in nutrient-poor environments. Hartmann (1951; cited in Sutton 1969) equated highly branched root systems with fertile soils and elongated, slender roots with unfertile soils (see section on environmental constraints).

Spatial variation in E, and in the morphological characteristics that determine E, depends upon the species composition of the plant community. In particular, the nature of the mycorrhizal association varies between the ectomycorrhizae (EM) and the arbuscular mycorrhizae (AM), and most plant species appear to have predominantly one form or the other rather than both (Gerdemann 1974). Morphological features of these forms are highly distinct, but little comparative information is available on systematic differences between EM and AM in either quantitative morphology or nutrient uptake efficiency.

Physiological characteristics

Nutrient absorption by roots and mycorrhizae depends upon the gradients in nutrient concentration with the soil-mycorrhizosphere-root system and the physiological processes of water and ion transport. The physiological characteristics that influence the efficiency of soil resource acquisition by mycorrhizae include the metabolic costs of growing and maintaining root and fungal tissues as well as the nutrient transport activity. Thus, the physiological indices required to improve our conceptualization of mycorrhizal dynamics include measures of nutrient absorption rate and respiration rate, ideally including the activity of extramatrical hyphae which clearly affect the uptake process (Finlay 1985).

Several insights about likely patterns of variation in the physiological component of E can be gleaned from the extensive literature on nutrient uptake by plants. First, ion uptake is an energy-requiring process (Bowling 1976) and some evidence indicates that a significant proportion (10–30%) of root respiration may be associated with ion uptake (van der Werf et al. 1988). Second, the environmental conditions encountered by roots profoundly affect the energetic requirements of nutrient uptake (Thompson and Troeh 1978), and the intrinsic root demand may vary inversely with nutrient availability (Dighton and Harrison 1983). Third, nutrient uptake activity varies markedly with the age and morphological state of roots (Chung and Kramer 1975), including mycorrhizal type or species. Fourth, some EM probably directly regulate nutrient availability through the enzymatic mineralization of organic matter (Trojanowski et al. 1984), though the significance of this mechanism remains to be conclusively demonstrated in field situations. Finally, any ability of senescing roots to retranslocate stored nutrients could affect E. Nambiar (1987) has suggested that this is unimportant, but Newman (1985) indicated that inter-root transfer of nutrients from senescent to active roots via mycorrhizal hyphae may be significant.

The influence of mycorrhizae on the balance between uptake and the respiratory costs of nutrient acquisition remains controversial and undoubtedly varies among plant and fungal species, across sites and between plant life history stages. Fitter (1989) has argued that AM only benefit the host plant during those brief intervals when demand for P is relatively high, but the ubiquity of EM in many temperate forest ecosystems would seem to signal a central role in regulating E.

Root longevity

In the same way that leaf lifespan affects the cost-benefit ratio of plant investment in foliage (Mooney and Gulman 1982), fine root longevity influences the efficiency of soil resource acquisition (Orians and Solbrig 1977). Currently, both theory (Grime 1977; Orians and Solbrig 1977; Caldwell 1979; Chapin 1980) and empirical evidence (Aber et al. 1985) support the contention that root longevity increases with decreased site fertility; particularly long-lived root systems have been observed (over 5 years) in nutrient-poor pine forests (Orlov 1968; Trappe and Fogel 1977; Fahey et al. 1985). Root longevity also may depend upon spatial variation in soil nutrient availability and McKay and Coutts (1989) have argued that high fine root turnover should be associated with heterogeneous soils, as access to favorable sites would be maximized. Finally, the costs of maintaining and protecting mycorrhizae in the face of herbivory (Ausmus et al. 1977) and environmental stress, together with age-related declines in the capacity for nutrient absorption, probably determine the optimal timing of root sloughing.

Environmental constraints

The efficiency of nutrient acquisition by any individual root will be constrained by the rate of resource supply from the soil microsite in which it is located, and for the whole root system by the distribution and growth of roots through heterogeneous soils. An effective strategy for optimizing the efficiency of resource acquisition by the whole root system would include an effective means of encountering resource-rich sites (St. John et al. 1983), proliferating absorbing surface area within those microsites (Drew 1975), and adjusting physiologically to the localized soil enrichment (Jackson et al. 1990). Thereafter, the duration of high resource supply from these microsites might determine the longevity of fine roots. Thus, the spatial placement of the fine root system, regulated both by the soil environment and by genetically determined constraints on root system form (Toumey 1929; Sutton 1969), influences the root system efficiency in soil resource acquisition.

Table 1. A simple example of calculating the sensitivity of the efficiency of soil nutrient acquisition by fine roots for organic and mineral horizons of a northern hardwood forest soil (adapted from H. McKay, personal communication)

I. Standard conditions: carbon cost of 1 g of fine roots

Carbon content of roots = 500 mg C/g root
Growth respiration = 140 mg C/g root
Maintenance respiration rate = 2.0 mg C/g per day
Longevity = 300 days

Total carbon cost = 1.24 g C

II. Standard conditions: nutrient gain by 1 g roots

	Organic horizons	Mineral horizons
Specific root length (see Fig. 2)	4000 cm/g root	1500 cm/g root
Rooting density	50 mg root/g soil	1.4 mg root/g soil
Effective soil mass for 1 g roots	20 g	715 g
N mineralization rate	10 μg N/g per day	0.05 μg N/g per day
Total N mineralization (= uptake)	60 mg N	10.7 mg N

III. Standard conditions: efficiency $= \frac{\text{nutrient gain}}{\text{carbon cost}}$

Organic horizons	Mineral horizons
E = 48.4 mg N/g C	E = 8.6 mg N/g C

IV. Sensitivity of E

Variation in longevity

Organic		Mineral	
Longevity	E	Longevity	E
50 days	13.5	50 days	2.4
100 days	23.8	100 days	4.2
200 days	38.5	200 days	6.9

To illustrate the sensitivity of E to variation in these components, I offer a simple example for mycorrhizae in organic and mineral soil horizons at HBEF (Table 1). In this northern hardwood forest the value of E is sensitive to root longevity, increasing by about 50% for a doubling longevity. Also, roots in the organic horizons have much higher E than those in mineral horizons (Table 1), and about half of this difference appears to be accounted for by the higher specific root length of the organic horizon roots (Fig. 2).

Several potentially important effects are not accounted for in the simple example in Table 1. First, overlapping nutrient depletion zones, convective transport, and spatial and temporal variation in mineralization and immobilization are important in most soils and would significantly affect E (Nye and Tinker 1977). Second, it seems likely that covariation exists among the characteristics of roots and mycorrhizae, particularly age, morphology, respiration, and uptake rates; unfortunately, little quantitative information is available in this regard. Finally, because of the energetic cost of maintaining fungal tissues, the trade-offs between retention of mycorrhizal roots versus building of new roots are more complex than this simple example portrays. The difficulties of obtaining empirical evidence to improve this conceptualization has limited its quantitative development, but ecosystem manipulations like the ones below promise future advances.

Soil fertility and carbon allocation to mycorrhizae

The most prominent envionmental gradient regulating the dynamics of mycorrhizae is soil fertility. The effect of high soil nutrient supply (particularly P) in suppressing mycorrhizae formation is well known (Mosse et al. 1981) and might be regarded as a special case of the more general decline in belowground C allocation hypothesized under conditions of high soil resource supply (Thornley 1972; Wareing and Patrick 1975). If plant nutrient requirements can be met with smaller investment in mycorrhizal tissues, then increased aboveground allocation will lend a competitive advantage in the scramble for canopy space and light resources or allow more prolific fruiting.

Current evidence for some coniferous forests indicates that fine root biomass may be higher on infertile than fertile sites (Keyes and Grier 1981) and that the principal mechanism explaining increased aboveground growth in response to fertilization is a relative decrease in C allocation (Grier et al. 1985; Gower et al. 1992). In contrast, calculations of Nadelhoffer et al. (1985) suggested that belowground C allocation in mixed hardwood and conifer stands in Wisconsin increased with increasing fertility and productivity so that the proportion of allocation belowground remained constant or actually increased with increasing nutrient availability. Moreover, in a 90-year-old northern hardwood stand in New Hampshire, fertilization greatly increased fine root biomass (Safford 1974). These contrary results may be explained in part by the aforementioned question of fine root longevity; higher fine root biomass may signal either higher production or greater longevity. However, the response of C allocation patterns to increasing fertility may be fundamentally different between western conifer and northern hardwood forests (Gower et al. 1992).

Recent studies of fine root dynamics in northern hardwood forests at HBEF illustrate some of the principles described above and indicate that our ability to quantify E in field situations remains limited. My approach was to emplace nylon-coated, fiberglass screens (hole size = 4 mm^2) in the forest floor in late spring by removing the O_i litter down to the top of the rooting zone in the O_e. Litter was then replaced over the screens and the corners flagged. About 2–4 weeks later the position and morphology of three or four fine roots were recorded near each corner of the in situ screens. These samples were revisited in August and October. Measurements were not possible in a second year because the large number of accumulated roots early in the second summer often made unambiguous identification of individual roots difficult (some artificial pruning would be needed to facilitate identification of individual roots). Root growth through screens was also measured by removing the entire overlying O_i layer at the time of initial measurements (early summer), counting the number of intersecting roots, and replacing the O_i litter. Subsequent measurements on these screens only quantified the net changes in the number of live and dead roots (see below). All these root screen measurements were made during cool, moist periods to avoid desiccation damage.

Fertilization at small scale resulted in greater increases in fine root growth as trees allocated C to the enriched microsites. Our procedure was to make biweekly additions of complete, liquid fertilizer (at rate of 1.2, 0.3, 1.3, 0.8 g/m^2 of N, P, K, Ca, respectively) to 20 × 20 cm plots overlying 25 in situ screens during the interval 10 July to 18 September (i.e., six applications). Root growth increased six-fold in comparison with control screens. However, fine root mortality also increased, as only about 50% of the roots mapped in fertilized screens survived until late summer (August), compared with 76% survival on the control screens. Taken together with the observations of Aber et al. (1985) that fine root longevity increased with decreasing N availability in Wisconsin, it appears that the response to fertilization and fertility gradients in eastern hardwood-conifer forests may involve both increased production and increased turnover. Reconciling these observations with the contrasting responses noted for western conifers and the fertilization response of Safford (1974) will require additional research.

Fine root longevity and decomposition

A summary of existing literature on fine root biomass and production in world forests (Vogt et al. 1986) and the study of Aber et al. (1985) suggest that values of fine root longevity in many temperate forests are about 1 year. Our direct observations for the in situ root screens at HBEF over two growing seasons indicated that fine roots in the northern hardwood forest live somewhat longer than 1 year. These values are difficult to reconcile with observations of fine root decay in eastern hardwood and conifer forests (McClaugherty et al. 1984) including HBEF (Fahey et al. 1988). That is, observed decay rates are much too low to accommodate estimates of fine root mortality unless organic matter accumulation rates are high. Periodic surveys at HBEF, however, indicate that forest floor organic matter has remained constant over the past 15 years in this approximately 70-year-old northern hardwood stand (T. G. Siccama, unpublished work).

Three possible explanations for this paradox of high root mortality and slow decay in northeastern forests are: (1) root decomposition estimates are too low; (2) herbivory of fine roots is an important mechanism of root mortality; and (3) root longevity estimates are too low. The incubation of fine roots in mesh bags might alter the decay process; however, Fahey et al. (1988) tethered fine roots (0.5–1.0 mm diameter) and measured their decay in direct contact with soil, and decay rates were not much different than for roots incubated in mesh bags. Perhaps the removal of fine roots from their intricate mycorrhizosphere environment, and the severing of extramatrical fungal hyphae during processing for decay studies, alters the available microflora and the soil structure to the extent that decay rates are reduced. Because many EM fungi may be capable of decomposition activity (Trojanowski et al. 1984), they may become involved in fine root decay upon the death of root tissues; it is notable that Harley (1937) observed proliferation of mycorrhizal hyphae through the cortex of moribund fine roots.

If herbivory by soil animals is a significant mechanism of root mortality, the presumably high rates of decay of animal fecal material might help to explain the paradox of root longevity and decay in northeastern forests. In summer 1990 we followed a cohort of about 600 fine roots at HBEF that had grown through the in situ screens in late May and early June. Subsequent remeasurement of these roots indicated that 27% had disappeared from the screens by early August and an additional 13% disappeared by October. The disappearance of roots in this brief time interval suggests herbivory. Supporting the latter explanation were observations of large numbers of potential root herbivores (especially slugs, white grubs and millipedes; Sutton 1969). Summer 1990 at HBEF was unusually wet; in contrast, in the more typical summer of 1989 only 5% of a cohort of 250 roots born in June had disappeared from in situ screens by October. Thus, based upon this limited evidence it appears that fine root hervibory is probably important but highly variable from year to year.

A contrasting result was obtained by Santantonio and Grace (1987), who developed a steady-state model of fine root dynamics in *Pinus radiata* forest in New Zealand based upon empirical observations of root production and decay. Their model indicated consistency between root production, mortality, and decay in that forest, where fine root decay rates were much higher than observed in forests of northeastern North America. Perhaps some unknown constraints on fine root decay that are associated with the acidic soils of northern, cold temperate forests do not exist in the favorable environment of the New Zealand sites.

Forest communities and their mycorrhizae

Vegetation composition may be the most important single factor regulating patterns in the fluxes of energy and nutrients in ecosystems. It seems likely that differences among plant species in fine root activity (and E) play a prominent role in determining how vegetation controls these ecosystem processes. However, differences among species of mycorrhizal fungi could also play an important role, and the community of mycorrhizal fungi associated with plant roots also varies across the landscape. For example, Nantel and Neumann (1992) recently demonstrated that the distributional ranges of mycorrhiza-forming basidiomycete fungi were narrower than their tree symbionts along soil gradients in northern hardwood-conifer forests in southeastern Canada. Because of the low host-specificity of AM fungi (Gerdemann 1974) the reverse probably would be true of AM-dominated communities. The effect on E of different mycorrhizal associations undoubtedly varies. For example, morphological features are routinely used to define mycorrhizal "species" (i.e., morphotypes; Zak 1973), and many of these morphological features, such as the abundance of extramatrical hyphae, probably influence E. Also, extramatrical hyphae appear to play an important role in formation and stability of soil aggregates (Perry et al. 1989; Miller and Jastrow 1990), which affect both hydrology and the processing of C and nutrients in soils. Thus, the patterns of variation in the features of mycorrhizal activity that profoundly affect biogeochemical cycling are probably more complex than the overlying pattern of vegetation.

Although a complex set of characteristics mediates the competition between AM- and EM-forming species, the many obvious differences between these types suggest that the mycorrhizae must be an important component. In particular, the more rapid formation of the EM symbiosis, its potential for decomposition activity (Lindeberg 1948; Trojanowski et al. 1984), the formation of EM rhizomorphs for long-distance transport, and the significant capacity for storage (Harley and Smith 1983) are features that likely confer a competitive advantage under certain environmental conditions and also affect biogeochemistry. Alexander (1983) noted that monospecific forests dominated by EM-forming species commonly accumulate slowly decomposing litter, suggesting that EM may create soil environment conditions that prohibit the entry of AM-forming species. The high proportion of fungal mantle tissue in EM-forming species growing in seasonally varying environments in the subtropics may represent an adaptation for nutrient storage under conditions of pulsed availability of soil resources (Hogberg 1986). Thus, the mycorrhizal associations appear to play a key role in determining the composition of vegetation communities and thereby regulating the patterns of flux of energy and matter in terrestrial ecosystems.

In summary, the influence of mycorrhizae on the patterns of energy and nutrient flux in terrestrial ecosystems is determined by a complex interaction between the rates of supply of mineral nutrients and E. The morphology, demography and physiology of mycorrhizae is expected to maximize E subject to constraints set by the soil environment and perhaps by other plant life history traits. Thus, the environmental gradients that regulate species composition also influence E. Unfortunately, the extent to which most of these mycorrhizal properties vary among plant species, mycorrhizal type (AM, EM, others) and species of mycorrhizal fungi remains unclear. The longevity of mycorrhizae is perhaps the only important feature for which systematic differences among plant species and ecosystems have been predicted (Grime 1977) and observed (Aber et al. 1985). A comprehensive theory of mycorrhizae and ecosystems must await better information on the other components affecting E.

Acknowledgements. This research was supported in part by NSF grant no. BSR-8717570. The author thanks Zhihua Xu and Cindy Wood for expert field and laboratory assistance; Ruth Yanai for exchange of ideas; and Steve Miller and Mike Allen for reviewing the manuscript.

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