Root morphology and mycorrhizal symbioses together shape nutrient foraging strategies of temperate trees

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Photosynthesis by leaves and acquisition of water and minerals by roots are required for plant growth, which is a key component of many ecosystem functions. Although the role of leaf functional traits in photosynthesis is generally well understood, the relationship of root functional traits to nutrient uptake is not. In particular, predictions of nutrient acquisition strategies from specific root traits are often vague. Roots of nearly all plants cooperate with mycorrhizal fungi in nutrient acquisition. Most tree species form symbioses with either arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) fungi. Nutrients are distributed heterogeneously in the soil, and nutrient-rich "hotspots" can be a key source for plants. Thus, predicting the foraging strategies that enable mycorrhizal root systems to exploit these hotspots can be critical to the understanding of plant nutrition and ecosystem carbon and nutrient cycling. Here, we show that in 13 sympatric temperate tree species, when nutrient availability is patchy, thinner root species alter their foraging to exploit patches, whereas thicker root species do not. Moreover, there appear to be two distinct pathways by which thinner root tree species enhance foraging in nutrient-rich patches: AM trees produce more roots, whereas EM trees produce more mycorrhizal fungal hyphae. Our results indicate that strategies of nutrient foraging are complementary among tree species with contrasting mycorrhiza types and root morphologies, and that predictable relationships between below-ground traits and nutrient acquisition emerge only when both roots and mycorrhizal fungi are considered together.

mycorrhizal fungi | plant traits | root proliferation | soil heterogeneity | symbioses

In recent years, there has been considerable progress in linking plant traits such as leaf thickness and wood density to various plant functions (1, 2), which can be of considerable value in scaling ecosystem processes to landscape and global scales (3). Plants also use a suite of approaches for acquiring nutrients from the soil, but an explicit link is lacking between nutrient acquisition and specific root traits. For example, nutrients are often heterogeneously distributed in soil due to the patchy distribution of litter and the activities of animals so that a precise foraging strategy that allows preferential root proliferation in nutrient-rich "hotspots" can provide greater nutrient returns for a particular carbon investment in roots (4–7). However, the precision of plant foraging for nutrients that are distributed in patches varies widely among species (8–12), and the cause of the variation and how it is linked to root traits remain unclear. Increasing evidence suggests that simple relationships between root construction and root function may need to include the symbiotic relationship between roots and mycorrhizal fungi (13, 14), which function together in nutrient acquisition (15).

Among the tree species of the world's forests, there is significant variation in the types of associated mycorrhizal fungi and in the construction of the absorptive roots (16). Species in the basal plant lineages, such as the Magnoliaceae, form arbuscular mycorrhizal (AM) symbioses (17). Ectomycorrhizal (EM) symbioses emerged among several of the more advanced lineages of plants (18). In many temperate forests, both AM and EM trees commonly co-occur despite fundamental differences in nutrient acquisition strategies (19, 20). EM fungi are, on the whole, better adapted to acquire nutrients from organic substrates than AM fungi (21, 22). Thus, EM trees may exhibit greater dependence on mycorrhizal hyphal foraging than AM trees under conditions where nutrients largely occur in organic forms.

Moreover, absorptive roots of many species in the more recently diverged lineages tend to be thinner than those roots of species of more basal lineages (23). Recent studies suggest that the diameter of absorptive roots, which affects the carbon costs of constructing root length (24), also influences root foraging strategies for mineral nutrients (11, 12). Compared with species with thin roots, thick-root species often have longer root lifespans (25) but, at least in AM species, proliferate their roots more slowly in nutrient-rich patches (11, 12). Thus, there may be a trade-off between building long-lived, thick absorptive roots and rapid root foraging in ephemeral nutrient hotspots in AM species. However, because roots are mycorrhizal in the vast majority of cases, one needs to consider the mycorrhizal fungi, together with roots, when attempting to understand nutrient foraging (12, 15, 26). For example, when foraging in fertile patches that are relatively short-lived, there may be a greater advantage for plant species with costly, thick absorptive roots to rely more on mycorrhizal fungi than those plant species with less costly, thin roots because hyphae are typically much thinner and, presumably, much less costly than roots.

Significance

Plant growth requires acquisition of soil nutrients in a patchy environment. Nutrient patches may be actively foraged by symbioses comprising roots and mycorrhizal fungi. Here, we show that thicker root tree species (e.g., tulip poplar, pine) respond weakly or not at all to nutrient heterogeneity. In contrast, thinner root tree species readily respond by selectively growing roots [arbuscular mycorrhizal trees (e.g., maple)] or mycorrhizal fungal hyphae [ectomycorrhizal trees (e.g., oak)] in nutrient-rich "hotspots." Our results thus indicate predictable patterns of nutrient foraging among tree species with contrasting mycorrhiza types and root morphologies. These findings can pave the way for a more holistic understanding of root-microbial function, which is critical to plant growth and biogeochemical cycles in forested ecosystems.

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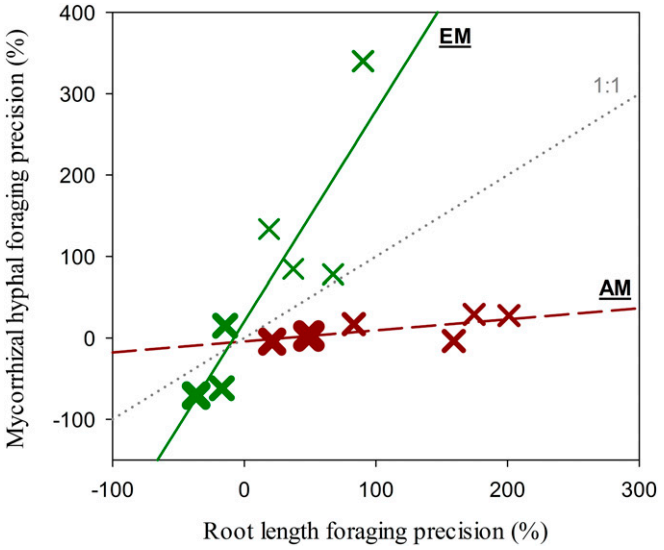

Fig. 1. Foraging precision of roots vs. extramatrical mycorrhizal fungal hyphae. Six AM (red color) and seven EM (green color) tree species are shown. The thickness of the symbol "x" is proportional to averaged root diameter of the first three root orders of the species. Species located above the 1:1 line suggest higher foraging precision in mycorrhizal hyphae than roots, whereas species located below the 1:1 line suggest higher foraging precision in roots than mycorrhizal hyphae. Precision of mycorrhizal hyphal foraging of EM fungi was positively correlated with EM root foraging precision (slope = 2.58, $r^2 = 0.76$, $P < 0.01$; $n = 7$), but AM hyphal foraging precision was similar among the tree species (slope = 0.14, $P = 0.16$; $n = 6$).

To understand better how nutrient foraging is influenced by the specific root and mycorrhizal traits, we examined the foraging strategies of both AM and EM tree species that exhibited wide variation in root morphology and architecture (Fig. S1 and Table S1). The experiment was conducted in a plantation where trees of the same species are planted in isolated and replicated plots (Fig. S2). Six AM and seven EM temperate tree species were selected (Fig. S3), and the diameters of their absorptive roots largely covered the range found in temperate and boreal trees. In particular, we examined the nutrient foraging precision of both roots and mycorrhizal fungal hyphae in these species. Using a root ingrowth method, we were able to estimate the preferential proliferation of newly grown absorptive roots [the most distal three orders (27)] and extramatrical mycorrhizal fungal hyphae [indicated by phospholipid fatty acid (PLFA) (28)] in ground-leaf nutrient hotspots compared with those roots or hyphae in unfertilized patches. Root or hyphal foraging precision was calculated as the percentage of increase in root length or hyphal biomass in leaf-amended soil over the percentage of increase in root length or hyphal biomass in unamended soil for each tree species over one growing season. Among the replicated plots of a given tree species, both roots and mycorrhizal fungal hyphae exhibited a fair degree of variation in foraging precision; we thus analyzed the mean foraging precision of a tree species.

Results and Discussion

We found striking differences in root and hyphal foraging precision between AM and EM tree species. In terms of root foraging precision, there was greater variation among AM tree species (21–201%) than among EM tree species (−36 to 90%; Fig. 1), despite a similar degree of variation in root diameter among tree species within a mycorrhiza type (Table 1). In terms of hyphal foraging precision, however, there was greater variation among EM tree species (−70 to 340%) than among AM tree species (−4 to 29%; Fig. 1). Using an alternate method of AM and EM fungal estimations generated overall similar results in the pattern of species foraging precision (Fig. S4). These results suggest, for the first time to our knowledge, the existence of two spectra in foraging strategies among temperate trees determined by their mycorrhiza types. Unlike the universal leaf economics spectrum of photosynthesis (1), we found two potential pathways (roots vs. hyphae) in nutrient acquisition. AM trees vary in their ability to forage selectively in nutrient patches primarily by varying root proliferation as a function of root diameter. In contrast, EM trees vary in their ability to forage selectively in nutrient patches primarily by varying mycorrhizal hyphal proliferation as a function of root diameter. There was comparatively little change in root biomass, root architecture, and percentage of mycorrhizal colonization of roots when trees species foraged in the nutrient-rich patches (Table S2).

Compared with root foraging, the use of mycorrhizal fungal hyphae may permit a more thorough exploitation of nutrient patches in soil (15). This prediction was supported for the EM trees, which showed greater hyphal foraging precision than root foraging precision in the majority of trees (average of 74% for hyphae vs. 21% for roots, five of seven tree species were above the 1:1 line; Fig. 1). EM trees may rely more on their fungal symbionts because some EM fungi are known to develop rhizomorphs that can extend many centimeters away from a root (29) and also have greater potential for mineralizing organic matter than roots or AM fungi (21). However, the situation was quite different for the AM tree species in our study. The mycorrhizal hyphal foraging precision was, on average, 10-fold lower than root foraging precision among all AM tree species (11% for hyphae vs. 115% for roots, all six tree species were below the 1:1 line; Fig. 1), and variation for AM hyphal foraging precision was more constrained than for EM hyphae (slope of regression line close to 0; Fig. 1).

Tree species with thinner roots generally exhibited greater foraging precision than tree species with thicker roots, mostly due to mycorrhizal fungal hyphae in EM tree species or roots in AM tree species (Fig. 1). These findings are consistent with a lifespan-plastic foraging tradeoff, where species with thinner and

Table 1. Root diameter of 13 temperate tree species from a plantation in the eastern United States

Mycorrhiza type	Species	Abbreviation	Root diameter, mm
AM	*Acer negundo*	Acne	0.29
	Acer saccharum	Acsa	0.29
	Prunus serotina	Prse	0.35
	Juglans nigra	Juni	0.36
	Sassafras albidum	Saal	0.61
	Liriodendron tulipifera	Litu	0.83
Mean			0.45
CV%			48%
EM	*Carya glabra*	Cagl	0.19
	Quercus alba	Qual	0.19
	Quercus rubra	Quru	0.21
	Betula alleghaniensis	Beal	0.24
	Picea rubens	Piru	0.45
	Pinus virginiana	Pivi	0.46
	Pinus strobus	Pist	0.63
Mean			0.34
CV%			51%

Diameter represents the average of roots of the first three orders in both nutrient-rich and nutrient-poor patches. The mean and coefficient of variation (CV%) are also shown in the group of AM and EM tree species.

shorter lived roots more precisely forage for nutrients in short-lived nutrient hotspots (30). However, whether they use roots or hyphae depends on their mycorrhizal type. After accounting for the effects of root diameter using analysis of covariance (ANCOVA), AM roots, on average, foraged more precisely than EM roots (average of 130% vs. 7%; $P < 0.001$), suggesting an overall greater dependence on root foraging by AM trees than by EM trees. In addition, for those species with precise foraging strategies (species with thinner roots), root production per ingrowth core was higher in AM trees than EM trees (Fig. S5), suggesting AM tree species invest more carbon in constructing foraging roots than EM tree species. In contrast, although thinner rooted EM trees foraged with their hyphae more precisely than thinner rooted AM trees (Fig. 1), the overall average hyphal foraging precision (independent of root diameter) was not significantly different between EM and AM tree species (60% vs. 28%; $P = 0.57$). It is worth noting that we included only two major lineages of EM trees (Pinales and Fagales) in this study, and that the patterns we observed could be different for other lineages. Also, thickness of absorptive roots is generally phylogenetically conserved (23), so that caution is needed in interpreting the diameter effects across a wider range of species than examined here. Nevertheless, these two lineages represent a very large fraction of EM tree species in temperate and boreal ecosystems.

In contrast to the predictable relationship of root traits with foraging precision across tree species, absolute root length density or mycorrhizal hyphal biomass was species-specific (Fig. 2, Fig. S5, and Tables S2 and S3). The low foraging precision in AM tree species with relatively thick roots is associated with low root length production in both bulk soils and nutrient hotspots. In contrast, some of the EM tree species with relatively thick roots produced a significant amount of root length and mycorrhizal hyphal biomass even in unfertilized soils. The low foraging precision for these EM tree species (Pinales species in this study) mainly resulted from the small or even negative stimulation of their roots or mycorrhizal fungal hyphae to localized nutrient enrichments over the roots or mycorrhizal fungal hyphae in unamended soil (Fig. 2). Supplementation of soil with leaves slightly decreased the moisture content in the ingrowth cores (Fig. S6) and, consequently, could have resulted in underestimations of foraging precision for all species if soil moisture was equivalent between the two treatments. These differences in soil moisture may have also contributed to the negative values for some low-precision species.

The limited response in root and hyphal proliferation in nutrient hotspots of members of the Pinales (thick-root EM trees) could reflect an adaptation to environments with near-homogeneous soil nutrients, which could be created by recalcitrant coniferous leaf litter that accumulates over many years instead of rapidly decomposed litter that comes in brief annual pulses (e.g., leaf litter of *Betula*). Here, we suggest that the foraging precision of a plant species may be considered as a plant trait that is responsive to variation in soil nutrient availability, and thus may possibly play a role in species distributions. For example, species with low foraging precision (in terms of either roots or hyphae) may prefer habitats where soil nutrients are largely spatially and temporally homogeneous. In contrast, species with high foraging precision could be relatively competitive in environments where nutrient heterogeneity is strong in both space and time, such as where there is more disturbance of vegetation or soil. Our result of diverse responses in roots and mycorrhizal fungi to nutrient addition among tree species also suggests that use of the commonly adopted ingrowth-core technique to measure root and mycorrhizal fungal production (31) could introduce bias. In particular, studies using sand cultures with limited nutrient supply (32) may underestimate mycorrhizal fungal production to varying degrees, depending on the mycorrhizal type and root thickness of host tree species.

There is increasing evidence from field experiments and modeling simulations that mycorrhizal fungi play a key role in the biogeochemical cycles of terrestrial ecosystems (33). Forests dominated by trees of contrasting mycorrhiza types may differ in their nutrient economies (19), and thus ecosystem functions, such

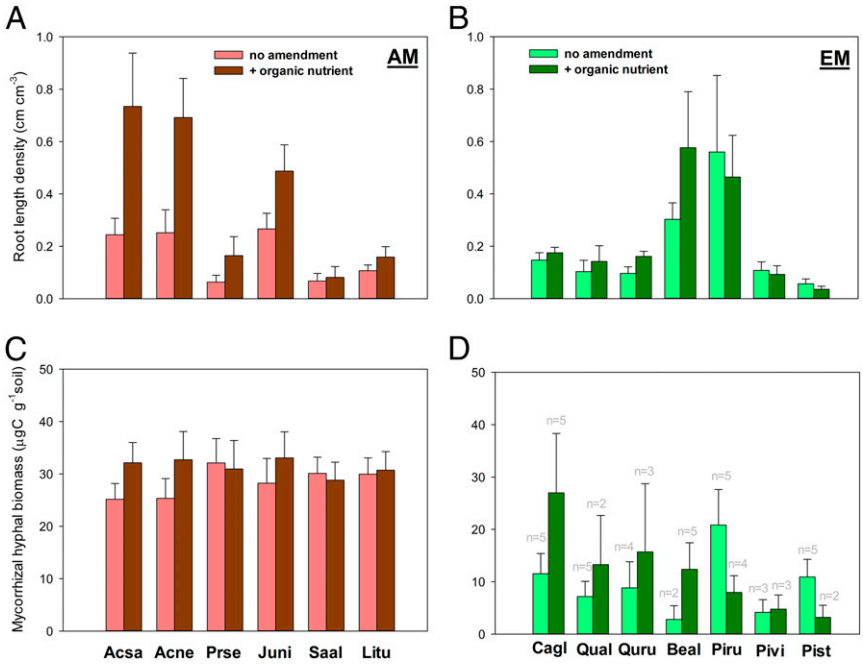

Fig. 2. Species root length density and extramatrical mycorrhizal hyphal biomass under two nutrient treatments. Six AM (*A* and *C*; red color) and seven EM (*B* and *D*; green color) tree species were studied using an ingrowth method for one growing season. Bars with light colors represent unfertilized treatment, denoted by "no amendment," and dark colors represent supplemented organic nutrients, denoted by "+ organic nutrients." Error bars represent SEM ($n = 8$ for *A* and *B*, $n = 7$ for *C*; in *D*, sample size is denoted on each bar). Complete scientific names of trees are provided in Table 1.

as soil carbon storage (34), nitrogen leaching (35), and phosphorus cycling (36). Here, we provide additional evidence that the relative dominance of AM or EM trees in a forest, as well as their root traits, may partly determine the response pathways (roots vs. hyphae) to fine-scale spatial heterogeneity of soil nutrients. These responses by roots and hyphae may, in turn, play a critical role in the ecosystem carbon and nutrient cycles and ecosystem community dynamics. This result also implies that global changes (e.g., atmospheric nitrogen deposition, climate warming) that alter forest species composition could affect soil carbon and nutrient dynamics at regional to global scales by altering the belowground foraging strategies of mycorrhizal symbioses. Furthermore, we show that the different acquisition pathways between contrasting mycorrhiza types and root morphologies provide potential complementarities in nutrient foraging strategies among trees, which may help to explain the coexistence of diverse species in temperate forests.

The finding (Fig. 3) that mycorrhiza type and root morphology mainly affect the foraging strategies of roots and mycorrhizal fungal hyphae of a tree species can also contribute to simulation studies on ecosystem functions. These two traits are often relatively easy to determine in the field in comparison to other traits, such as fine root length density or extramatrical hyphal production, and they are often phylogenetically predictable (17, 23). In addition, the recent advance of remote sensing that can differentiate forests dominated by AM-associating trees and forests dominated by EM-associating trees (37) presents the opportunity to scale up the findings in our field measurements of species nutrient foraging to landscape and global scales. Thus, our results provide a preliminary guide for simulation studies to predict ecosystem and global responses of roots and mycorrhizal fungi to future nutrient conditions based on simple traits, such as root diameter and mycorrhiza type. Furthermore, the previous conceptual framework suggests that a plant's mycorrhizal association (AM or EM) represents a "trait integrator" for a suite of functional traits involved in coupling carbon-nutrient cycles (19), and, here, we showed that the incorporation of root thickness to such a framework may further reduce uncertainties in simulation studies where mycorrhizal functions are incorporated (38). Therefore, an integrated description of both specific root and mycorrhiza traits will improve the holistic understanding of nutrient acquisition strategies across diverse tree species, and the prediction of biogeochemical cycling under global change scenarios.

Materials and Methods

Study Site and Species Selections. The common garden site was located at the Russell E. Larson Agricultural Research Center in central Pennsylvania (40°42′ N, 77°57′ W), which has previously been described in detail (25). The site was used as a grass hayfield before the planting of 1-y-old seedlings in 1996. The Hagerstown silt loam soils are well drained with moderate fertility. Soil pH ranges from 6.1 to 6.5. The common garden consists of 16 tree species planted in eight replicate blocks. In each block, each of the 16 species was planted in monospecific plots containing six individual trees aligned in two rows and spaced 3 m apart with 5 m of spacing between neighboring plots (Fig. S2). Each plot was trenched and isolated with plastic film to minimize root encroachment between plots. Thirteen species were selected in this study, including six AM and seven EM species (Table 1 and Table S1). At the time of the study, most trees were between 10 and 18 y old. Previous studies have shown large variation in root morphology, chemistry, and lifespan of the species in the common garden (25).

Ingrowth Experiment. An ingrowth experiment was conducted in the common garden plantation during the growing season of 2013. In early June, eight random locations were selected within each plot of the selected species, and a soil auger (3.5-cm diameter) was used to create a 10-cm deep soil core. Roots were removed from the cores using a 2-mm sieve. Root-free soil was homogenized within each plot and placed into eight ingrowth containers made from a plastic mesh tube (3.5-cm diameter, 10-cm length, and 4-mm aperture). Half of the containers were supplemented with 5 g of finely cut, oven-dried leaf material in the first one-third depth of the container (forming an organic layer about 3 cm deep) to serve as organic nutrient-rich patches. The leaves that were used were harvested from the selected 13 common garden tree species right before the experiment. Leaves from all species were mixed well with an equal proportion in dry mass for each species. These dry leaves can be considered as slow-release organic fertilizers that imitate naturally formed patchy nutrients, and plant responses in this study may not be directly comparable to findings using mineral fertilizers. Control containers contained only sieved soil with no nutrient amendment. All containers were placed upright back into the soil (top 10 cm) of the plot the same day that soil cores were collected. Thus, there were four ingrowth cores with organic nutrient additions and four controls with only sieved soil in each plot for all of the selected species, with eight replicates per species. After a few weeks, all soil cores were topped off with sieved soil (if needed) to make a level surface with the plantation floor. All ingrowth containers were harvested at the beginning of November in 2013. The limited variation in environment because of a single location and the relatively modest number of species in this study, as well as the lack of multiple years of data, are reasons to be cautious about extrapolating the results too widely.

Unlike AM fungi, which can be estimated from an AM-specific PLFA biomarker, EM fungi and non-EM saprotrophic fungi share the same fungal-specific PLFA biomarkers. To estimate the EM and non-EM saprotrophic fungal biomass (details are provided in *Measurement of Roots and Mycorrhizal Fungi*), we installed additional ingrowth containers in a mycorrhiza-free environment (by excluding roots) in the plots of EM tree species. Four PVC tubes 10 cm in diameter and 20 cm long were installed in the soil, and two nutrient-amended and two unamended ingrowth containers were then placed within the PVC root-exclusion tubes (using the same procedures described above). A small hole was drilled on the above-ground part of the PVC tubes (right above the soil surface) to prevent excess water retention within the tubes.

Eight measurements of soil moisture (volumetric water content) were conducted from July to October 2013. For each measurement, a random block (including all 13 species) in the common garden was chosen and all of the 132 ingrowth cores of the block were measured by a time-domain reflectometer

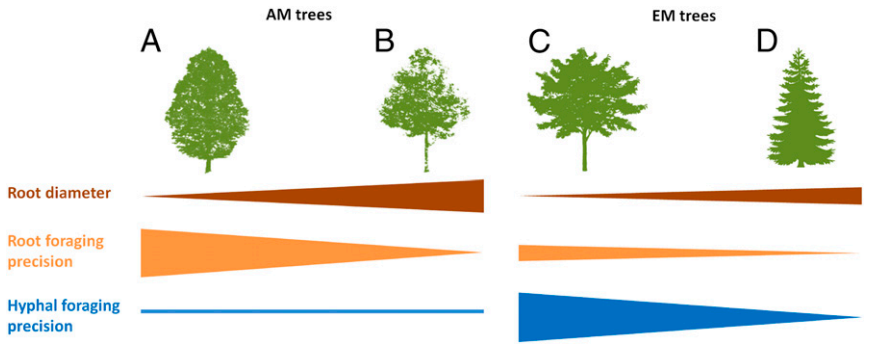

Fig. 3. Diagram showing the relationship between the mycorrhiza type, root diameter, and foraging precision of roots and mycorrhizal fungal hyphae. Some tree species, such as maple (*A*) and tulip poplar (*B*), associate with AM fungi, whereas others, such as oak (*C*) and pine (*D*), associate with EM fungi. Triangles depict simplified variation in patterns of the foraging precision of roots and mycorrhizal fungal hyphae roots with increasing root diameter.

using a 10-cm-long waveguide (TDR 100; Campbell Scientific, Inc.) (39). For the ingrowth cores in plots of EM species, soil moisture of the additional cores within the PVC root-exclusion tubes was also measured.

Our ingrowth experiment included hyphal proliferation associated with newly ingrown roots as well as with roots outside the soil core, which is realistic when the roots and/or associated mycorrhizal fungal hyphae encounter nutrient-rich patches. Hyphae were all considered exploration hyphae and likely linked to the common mycelial network within the whole plot. The access of hyphae from existing roots and from newly proliferated roots within nutrient-rich patches provided additional evidence of hyphal foraging for organic nutrients that is distinct from previous pot or growth chamber studies (13, 14). We also did not remove hyphae from the soil cores before installation because we believe that in natural ecosystems, nutrient patches derived from litter decomposition should include significant amounts of saprotrophic fungi, which may be competing with the mycorrhizal symbioses for nutrients (19). Although this preexisting fungal biomass may have led to bias in the estimate of absolute AM or EM hyphal proliferation within the patch, it was not confounded between the nutrient-addition treatments (calculation of "foraging precision" in *Materials and Methods*, *Statistics*).

Measurement of Roots and Mycorrhizal Fungi. After harvest, all ingrowth cores with the same nutrient treatment within one plot were pooled and well mixed. A subsample of soil (~100 g) was kept frozen (–20 °C) for later soil processing. The remaining soil was carefully rinsed in a 2-mm sieve to collect roots. Most of the roots collected were from the tree species within the plots; only a very small fraction of roots (<5% length on average) were from understory herbaceous and/or roots invaded from nearby plots (determined by root morphology, architecture, and color). Nontarget roots were discarded in later root processing. In addition, we considered the first three orders of roots to be absorptive roots, and only they were considered in this study (26).

About half of each root sample (indicated by fresh weight) was selected for scanning on a desktop scanner, and images were processed with WinRHIZO (Regent Instruments, Inc.) to determine the average root diameter and total root length. The other half was oven-dried (65 °C for 72 h) and weighed. Total root length and root dry weight were then calculated based on fresh weight fraction. Specific root length (SRL) was calculated as the ratio between total root length and root dry weight. The number of first-, second-, and third-order roots was determined, and branching ratios were calculated as the number of first-order roots per each second-order root (BR1-2) and the number of second-order roots per each third-order root (BR2-3). After scanning, the root subsample was preserved in 70% (vol/vol) ethanol for later determination of the percentage of mycorrhizal colonization. For roots of AM species, the percentage of length that was colonized by mycorrhizal fungi was determined using the line-intersect method (40). For roots of EM species, the percentage of root tips that were colonized by mycorrhizal fungi was estimated by inspection of root tip, color, architecture, and anatomy.

For PLFA analysis, about 5 g of freeze-dried soil was used for fatty acid extraction, and PLFAs of different biomarkers were quantified by gas chromatography (27). Extramatrical AM hyphal biomass was estimated using the PLFA biomarker 16:1ω5*c*. Although the biomarker 16:1ω5*c* is also found in bacteria (41), this background error should be the same for each species because the soil was the same for all species within the plantation. In addition, because there are no specific PLFA biomarkers for EM fungi only, we calculated the extramatrical EM hyphal biomass by subtracting the estimates from fungal biomarkers (18:1ω6, 18:2ω9) in the soil outside from the estimates from fungal biomarkers inside the PVC tubes from the same nutrient treatment. We also calculated the AM and EM fungal PLFAs using an alternate method, with AM plots as EM controls and EM plots as AM controls, assuming that they share similar bacteria and saprotrophic fungi

$$\textit{AM fungi in AM plots} = \textit{16:1}\omega\textit{5c in AM plots} - \textit{16:1}\omega\textit{5c in EM plots},$$

$$\textit{EM fungi in EM plots} = (\textit{18:1}\omega\textit{6} + \textit{18:2}\omega\textit{9})\textit{in EM plots} - (\textit{18:1}\omega\textit{6} + \textit{18:2}\omega\textit{9})\textit{in AM plots}.$$

Statistics. The root morphology (root diameter and SRL), architecture (BR1-2 and BR2-3), and mycorrhizal colonization, as well as proliferation of roots (length and biomass) and extramatrical hyphae, were analyzed with two-way ANOVA to determine the effects of tree species and nutrient treatments in AM and EM tree species separately. The relationships between root diameter and root or hyphal proliferation were determined by regression analysis of root diameter vs. root length, biomass, extramatrical hyphal biomass, and mycorrhizal colonization. Foraging precision of root length and hyphae biomass was calculated as the percentage of increase in organic patches compared with control patches

$$\textit{Root foraging precision}(\%) = 100 * (\textit{Root length}_{organic} - \textit{Root length}_{control}) / \textit{Root length}_{control},$$

$$\textit{Hyphae foraging precision}(\%) = 100 * (\textit{Hyphal PLFA}_{organic} - \textit{Hyphal PLFA}_{control}) / \textit{Hyphal PLFA}_{control}.$$

The relationships between root foraging precision and extramatrical hyphal foraging precision were determined by regression analysis in AM and EM groups separately. In addition, the correlations between foraging precision (either root length or hyphal biomass) and root diameter, as well as the effect of different mycorrhiza type (AM vs. EM) on foraging precision, were determined with ANCOVA. All statistics were performed using R (version 3.02; R Foundation for Statistical Computing; www.r-project.org).

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