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0014-4754/91/040350-06$1.50 + 0.20/0

Mycorrhizas and root architecture

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Summary. Roots function dually as a support system and as the nutrient uptake organ of plants. Root morphology changes in response to the soil environment to minimize the metabolic cost of maintaining the root system, while maximizing nutrient acquisition. In response to nutrient-limiting conditions, plants may increase root fineness or specific root length (root length per gram root weight), root/shoot ratio, or root hair length and number. Each of these adaptations involves a different metabolic cost to the plant, with root hair formation as the least costly change, buffering against more costly changes in root/shoot ratio. Mycorrhizal symbiosis is another alternative to such changes. Plants with high degrees of dependence on the symbiosis have coarser root systems, less plasticity in root/shoot ratio, and develop fewer root hairs in low-fertility soils. In nutrient-limited soils, plants highly dependent on mycorrhiza reduce metabolic cost by developing an even more coarse or magnolioid root system, which is less able to obtain nutrients and thus creates a greater dependence of the plant on the symbiosis. These subtle changes in root architecture may be induced by mycorrhizal fungi and can be quantified using topological analysis of rooting patterns. The ability of mycorrhizal fungi to elicit change in root architecture appears to be limited to plant species which are highly dependent upon mycorrhizal symbiosis.
Key words. Root morphology; vesicular-arbuscular mycorrhizal fungi; phosphorous; branching pattern; root architecture.

Introduction

Root biomass is the most commonly reported parameter of root growth, and factors which affect root growth are frequently evaluated by measuring biomass change. Root biomass measurements taken alone, without consideration of how root material is allocated (i.e., root geometry and root architecture), may cause important changes and differences in biomass allocation to be overlooked. Although these differences and changes in root architecture may dictate the nutrient absorbing power of a root system, the latter cannot be assessed or inferred from root weight measurements. In fact, root weight generally correlates poorly with nutrient uptake capacity because the main axes, which contribute most of biomass, contribute least to nutrient uptake. Rather, it is the laterals, fine roots, and root hairs which perform most uptake tasks for the plant[3,27]. It is for this reason that it is important to study root architecture.

Mycorrhizal symbiosis can significantly improve plant nutrient acquisition in infertile soils. The hyphae of the mycorrhizal fungi are able to absorb more inorganic nutrients than roots alone, because the hyphae growing from the root can obtain nutrients beyond the zone of nutrient depletion which develops around roots. The hyphae also greatly increase surface area for nutrient absorption. A model has been proposed to describe optimal mycorrhization for a given root system in terms of cost-benefit analysis (Fitter, this issue). Recently, however, it has been suggested[11,21] that the vesicular-arbuscular (VA) mycorrhizal fungi (the most common type of mycorrhizal symbiont) alter plant root architecture and that such changes may also contribute to the nutrient uptake efficiency of mycorrhizal plants. In evaluating the effect of VA mycorrhizal fungi on plant root architecture, it is important to distinguish between direct effects of the mycorrhizal fungus on plant rooting strategy and those architectural changes which might occur indirectly as a result of the improved nutrient status of mycorrhizal plants. In this review, therefore, nutritional effects on root architecture are considered initially, followed by discussion of mycorrhizal effects and the relationship between them. The relationship between plant dependence on the symbiosis and mycorrhizal regulation of root architecture is also considered.

Nutritional effects on root architecture

Nutrient uptake by plants is related to soil parameters such as nutrient availability, buffering capacity, and mobility[7]. On the plant side, parameters such as root length, root diameter, root surface area:shoot weight ratio, and root hair density have been considered important for uptake of low-mobility ions such as phosphate[38]. The extent to which a root system branches will also affect the volume of soil explored for nutrient. The angle of branch roots (usually 60–90 degrees) is important because it ensures that lateral branches will grow beyond the zone of nutrient depletion whenever possible. Similarly, the radial angle of branches ensures that roots do not arise from the same poles, allowing greater volumes of soil to be explored for nutrients[12]. Clearly, the plant which produces the greatest interface with the soil has the greatest nutrient uptake potential, but this is balanced against the cost to the plant of growing and maintaining roots[12]. In this context, fine roots offer greater return for the investment, but fine roots have limited growth potential[28], lifespan[35], transport capacity, and are vulnerable to physical damage, desiccation, and grazing by soil-borne microarthropods or pathogens[12]. These limitations are overcome by increasing root diameter, but larger-diameter roots are more expensive to produce[12]. Fitter[12] has also clearly elucidated another set of compromises related to root morphology. An elongate, sparsely branched root morphology allows maximum exploration of soil volume for nutrients but this morphology is least efficient for nutrient transport to the shoot and represents the greatest energy expense to the plant. The highly branched, absorbing root morphology limits the volume of soil explored, but maximizes nutrient transport and cost efficiency. Superimposed on these considerations is the fact that for plants growing in competition with other plants (the normal condition), maximum nutrient uptake may be less important than rapid access to nutrients which deprive competitors of these nutrients. Clearly, interplant competition must be considered in any cost-benefit analysis of root morphology.

While innate genetic differences in root morphology exist for plant species, plants also differ significantly in their ability to alter root morphology in response to their environment. For example, bulk density and other characteristics of soil can elicit changes in root diameter[12,38]. Low soil water availability causes roots to adopt a more elongate, exploratory, less branched growth pattern. These changes in root geometry elicited by fluctuations in soil water were found to be far greater than those caused by varied nutrient availability (N and P)[12]. However, the impact of nutrient on root morphology should not be underestimated.

Roots of nitrogen-deficient plants branch extensively in regions where soil is rich in nitrogen. Length of lateral branch roots may also be longer in nitrate-deficient soil[12]. Low nutrient availability has also been shown to increase specific root length (root length per gram dry root weight) and root fineness[11]. Fertilization of phosphorus-deficient soil results in thicker roots with lower specific root length[33]. As might be expected, a threshold level of fertilizer exists above which no further changes in root morphology are observed. Presumably, the described changes in root morphology occur in response to nutrient stress and disappear when adequate nutrient is available for plant growth. In the absence of these changes in root fineness and specific root length, a more drastic response of increased root/shoot ratio may be

necessary for plant growth to continue under nutrient stress. In this respect, root hairs can be viewed as buffers to maintain root/shoot ratio[36].

As previously mentioned, root hairs are important morphological features of roots which facilitate and improve nutrient absorption in infertile soils, particularly for nutrients such as phosphorus which are relatively immobile[32]. Root hairs are less important for absorption of mobile ions because their uptake is limited by mass flow, not by diffusion. The advantage of root hairs is that they increase surface area for absorption of nutrients, resulting in higher nutrient inflow rates. For example, root hairs have been demonstrated to increase absorbing surface 6-fold for *Leucadendron laureolum* and 26-fold for *Hypolaena fastigiata*[27]. Economically speaking, the advantage of root hairs is the large increase in surface area per unit of biomass invested. Production of roots themselves for similar increases in surface area would consume much more biomass and therefore is rated as being metabolically more costly.

Root hair production maximizes uptake while minimizing dry weight[36] and may, in some cases, avoid a more costly increase in root/shoot ratio[42]. Since root hairs are relatively short-lived[26], they may be produced in response to periods of nutrient stress without long-term maintenance cost for the plant. For example, Foehse and Jungk[13] reported that when P levels in a nutrient solution were reduced from 100 to 2 μM, root hair length increased 3–7-fold and root hair density increased 2–4-fold, resulting in a 2–3-fold increase in root surface area. While root dry weight does not generally correlate well with shoot dry weight[3], Foehse and Jungk[13] found a high degree of correlation between root hair length and shoot dry weight. Since root hair length increases in response to P deficiency[5,8], increasing root hair length may be viewed as an adaptation to maximize shoot production in nutrient-limited soils. Thus, root hair length and density are not stable characters of species and may be altered to some degree by P availability.

Nevertheless, genetic differences among plant species in root hair density and root hair length are considerable. When root hair development of six diverse plant species was compared[24], Russian thistle (*Salsola kali* L.) had the greatest number and length of root hairs, followed by tomato (*Lycopericon esculentum* Mill.), lettuce (*Lactuca sativa* L.), wheat (*Triticum aestivum* L.), carrot (*Daucus carota* L.), and onion (*Allium cepa* L.), which had the fewest root hairs. Russian thistle had the thinnest roots and onions the thickest. Wheat and carrot had proportionately higher root/shoot ratios than the other species in this study. Since root hairs appear to have no effect on nutrient uptake in wheat[6], the greater root/shoot ratio observed for wheat[24] suggests that this species may compensate for its low root hair density by increasing root production to increase root surface area for absorption. Apparently, both increased root/shoot ratio and development of root hairs are strategies used by plants to acquire nutrients in infertile soils. Another alternative is the production of cluster-roots[27]. By producing bunches of roots in horizontal rows with long root hairs near the soil surface, these plants are able to trap nutrients as they enter the soil. Exudates from such clusters are fungistatic and ensure that plant energy is not lost to mycorrhizal symbiosis when it is superfluous[27].

Mycorrhizal effects on root architecture

An alternative strategy to cluster roots and other plant-mediated morphological adaptations is afforded by mycorrhizal symbiosis. In this symbiosis, plants provide organic nutrients to the fungal symbiont in return for inorganic nutrients absorbed by hyphae extending from roots into the soil. Thus, the surface area for nutrient absorption is greatly increased for the plant, the soil outside the zone of nutrient depletion is explored for nutrients, and root hair production is unnecessary. Indeed, dependence on the symbiosis is generally strongest in plant species which do not produce profuse root hairs and in species which produce relatively coarse roots of large diameter[4]. It is not surprising, therefore, that in the study conducted by Itoh and Barber[24] in which root hair development of six plant species was compared, species with the most abundant root hairs were ones which rely very little on mycorrhizal symbiosis for nutrient uptake. For example, russian thistle had the greatest root hair development and is typically nonmycorrhizal[30] while onions had the fewest root hairs and are highly dependent on the symbiosis[41]. Other typically nonmycorrhizal plants such as rushes, sedges, and grasses such as *Lolium perenne* L. also have highly developed root hairs[30].

While there appears to be a strong inverse relationship between root hair density or length and mycorrhizal dependency, the relationship between plant root/shoot ratio and dependence on mycorrhizaes is less clear. In studies comparing the dependence of 13 wheat cultivars, Azcon and Ocampo[1] observed among the cultivars fairly low levels of mycorrhizal dependence (i.e., −1.5 to 51.8% dependence) calculated as [(biomass mycorrhizal plant − biomass nonmycorrhizal plant) divided by biomass mycorrhizal plant] × 100. Generally, those wheat cultivars which lacked or had the least dependence on mycorrhizal symbiosis had the highest root/shoot ratios suggesting that, at least for this plant species, increased root/shoot ratio is an alternate strategy to dependence on mycorrhizaes. Cultivars which were somewhat dependent on the symbiosis had higher root/shoot ratios when mycorrhizal than when nonmycorrhizal. Such increases in root/shoot ratio could be viewed as detrimental to the plant because the metabolic cost of nutrient acquisition is higher if proportionately more root biomass is produced in response to the symbiosis. Mycorrhiza-mediated increase in root/shoot ratio contradicts the more common observations that mycorrhizal symbioses generally lower root/shoot ratio[2,9,10,17,18,23,31] or have no ef-

fect[29, 30]. That mycorrhizal fungi generally lower root/shoot ratios is further supported by Sanders et al.[37] who demonstrated that different mycorrhizal fungi lowered root/shoot ratios to different extents in the same host plant species. Since root/shoot ratios are also lowered by P fertilization, the effect of mycorrhizas on root/shoot ratio is probably nutritional[40] and an increase in root/shoot ratio may indicate an imbalance in the symbiosis. In the studies where mycorrhizal symbiosis resulted in decreased root/shoot ratio or did not affect root/shoot ratio, the plant species studied were ones which generally display high levels of dependence on the symbiosis. In contrast, wheat is a facultative mycotroph, and root/shoot ratio increased in response to mycorrhizal symbiosis. Further research will be necessary to determine whether level of dependence on the symbiosis is correlated with mycorrhizal effect on root/shoot ratios.

Warm-season grasses of the tallgrass prairie (obligately mycorrhizal plants) have relatively coarse root systems, display high levels of mycorrhizal dependency (> 98%)[20], and have root/shoot ratios that remain constant for both mycorrhizal and nonmycorrhizal plants[22]. Root/shoot ratios of cool-season tallgrass prairie grasses are also stable, despite the relatively low mycorrhizal dependence of these plant species. The relatively fine, highly branched root system of these cool-season grasses[20] apparently make the greater surface area for absorption of nutrient provided by mycorrhizal symbiosis unnecessary or less critical. In the case of wheat, however, the greater plasticity of wheat root/shoot ratios[1] and the generally higher root/shoot ratios of wheat compared with other crops[24], supports the hypothesis that altered root/shoot ratio is a distinct alternative to dependence on mycorrhizas for nutrient acquisition in a nutrient-limited environment. Greater plasticity in root/shoot ratio has also been observed by Koide et al.[25] in wild oat plants which are less dependent on mycorrhizal symbiosis than cultivated oats.

As previously mentioned, root weights and root/shoot ratios provide little if any information about the architecture of root growth. Unfortunately, there are relatively few studies which examine root architecture, particularly in relation to mycorrhizal symbiosis. It is clear that ectomycorrhizal fungi elicit profound changes in root morphology of host plants. In the presence of the fungal symbiont, short root elongation and root hair formation are suppressed and short roots swell and may branch dichotomously. These morphological changes can be simulated by exposure of roots to auxins and are reversed in the absence of the hormone. When the hormone is withdrawn, the more elongate short roots are densely covered with root hairs[39]. In contrast, it has been widely accepted that VA mycorrhizal fungi do not alter root morphology of hosts[14]. Certainly, the morphological changes in roots induced by VA mycorrhizal fungi are far more subtle than those caused by ectomycorrhizal fungi and seem to be related to architecture and branching patterns rather than gross suppression of lateral root growth.

To examine changes in root architecture, specific root length (SRL), expressed as root length per gram root biomass, is a useful parameter for a general indication of root morphology, because both root length and biomass are relatively easy to measure. Generally, young plants exhibit high SRL values, reflecting the small root diameter. SRL values decline as plants age and roots thicken. Plants grown in low fertility soils also have high SRL values, again reflecting the smaller diameter of the roots produced[11]. Presumably, the high SRL of young plants and plants in infertile soils allow maximum surface area for nutrient uptake. As plants mature and develop mycorrhizas which compensate for low nutrient availability in soil, SRL would be expected to decrease. Hetrick et al.[21] observed that SRL of *Andropogon gerardii* Vitm. was similar for all mycorrhizal plants at all the P levels tested. In nonmycorrhizal plants, however, SRL was 3–4-fold higher in soil receiving little or no P fertilizer, but was similar to mycorrhizal plants at high P levels. In a related study[34], SRL of cotton plants also decreased in response to mycorrhizal inoculation. More importantly, the most efficient mycorrhizal fungal species caused the greatest reduction in SRL. Thus, SRL provides important information about architectural changes caused by mycorrhizas. However, it does not provide any estimation of branching frequency, another important component of a plant's root strategy.

A method for assessing architectural change in root branching patterns by VA mycorrhizal fungi was first elaborated by Fitter[11]. Using graph theory from mathematics[16, 43], branching patterns of roots were quantitatively analyzed. This type of topological analysis considers root systems as mathematical trees, and pathlength or P_e is the total exterior pathlength of the tree representing the root system. P_e is assessed by summing the number of links from each lateral root tip basipetally to the root crown of the plant, with a link being the line connecting two branch points in a tree. For trees with the same number of terminal branches, P_e is a measure of branching patterns (fig. 1). Thus, trees with high values for P_e are representative of an elongate, sparingly branched root system. Such a root system will explore a greater volume of soil for nutrient. Trees with lower values of P_e depict highly branched root systems which are primarily absorptive in nature. These concepts are thoroughly reviewed by Fitter[11, 12]. Using topological analyses, Fitter[11] observed that both nonmycorrhizal and mycorrhizal plants of *Trifolium pratense* L. initially maintained an elongate, sparingly branched architecture. When nonmycorrhizal plants had developed 6–10 terminal branch roots, they adopted an absorptive, highly branched architecture while mycorrhizal plants did not adopt an absorptive growth pattern until 35 terminal branch roots had been initiated. The change in the mycorrhizal plants occurred when shoot P levels exceeded those of uninfect-

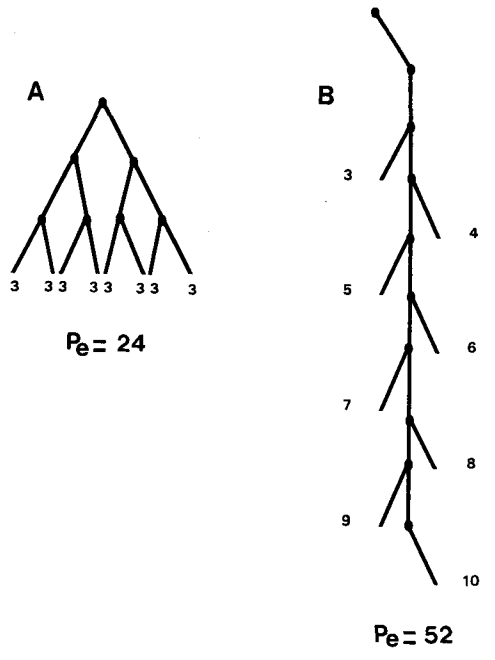

Figure 1. Topological analysis of branching patterns. Two root systems with 8 terminal root tips are depicted. The figure below each tip is the number of links between crown and tip. The sum of these figures, the total pathlength P_e, is lower for the highly branched root system *A* than for the sparingly branched root system *B*.

ed plants, implying internal plant control of root topology. Since increased branching is a general response of plants to increased supply of mineral nutrients [10], it was difficult to discern whether mycorrhizal effects on root branching were strictly nutritional or whether a unique mycorrhizal effect existed.

To distinguish between direct mycorrhizal effects and indirect nutritional effects on root system architecture, Hetrick et al. [21] studied the effect of mycorrhizal fungi, soil microorganisms, and P fertilization alone or in combination on pathlength of the tallgrass prairie grass, *Andropogon gerardii* Vitm. To facilitate pathlength analyses, models of trees were constructed, and equations were generated to estimate pathlength from the average number of primary, secondary, and tertiary roots per plant. A computer program for solving the equations was written in GW Basic. In this way, pathlength of the large number of plants in the various treatments could be compared using rather simple measurements, where the labor involved in direct quantification of all links in all root systems would have precluded topological analysis of such a large experiment. Since P_e is obviously influenced by plant size and number of tertiary roots, covariance analysis of pathlength using the number of tertiary roots as the covariate was necessary so that branching patterns only of similar-sized plants were compared.

In steamed soil and steamed soil amended with soil microorganisms, mycorrhizal plants displayed significantly higher P_e (reduced root branching) than nonmycorrhizal plants at the lower two or three P fertilization levels, respectively [21]. Plants grown in soils containing soil microorganisms also displayed somewhat greater pathlengths. However, these differences in pathlength were not simulated by P fertilization, implying that the effect of mycorrhizaes and to some degree that of other soil microorganisms are not strictly nutritional but could perhaps be hormonal. Thus, mycorrhizal plants appear to explore a greater volume of soil for nutrients, allowing hyphae to perform nutrient absorption for the plant. In this way hyphae act as the additional branches of the root system. Nonmycorrhizal plants, lacking hyphae for absorption, must themselves produce the finely branched network capable of nutrient acquisition [21]. In response to competition with other soil microorganisms for nutrient, mycorrhizal plants appear to explore an even greater volume of soil for nutrient, suggesting that mycorrhizal fungi are able to alter rooting strategy in response to rhizosphere and soil fertility. Plant nutrient content controls whether mycorrhizal symbiosis is established or maintained [15], the fungal symbiont then appears to control the pattern of root growth, positioning the roots to maximize symbiotic function [19]. These hypothesized, integrated controls on plant growth and symbiosis are summarized in a model (fig. 2).

Relationship of root architecture to plant dependence on mycorrhizal symbiosis

The integrated control of root architecture (fig. 2) has interesting ramifications. By reducing root branching, the mycorrhizal fungus induces changes in root architecture which make the plant less capable of independent nutrient absorption and consequently more dependent on the symbiosis [21]. This interpretation is supported by the responses observed by Price et al. [34] in studies of mycorrhizal fungal effects on cotton rooting structure. They found that when P availability was limited , extension of root branches slowed and frequency of branch initiation was reduced. Therefore, cotton responded to nutrient stress not by increasing root/shoot ratio but by developing a more elongate, sparingly branched, magnolioid root architecture. In adopting a magnolioid architecture, the ability of these plants to acquire nutrient is more limited and dependence on mycorrhizal symbiosis increases. Price et al. [34] concluded that increased mycotrophy when soil P is limited may be partially attributed to low soil P availability and also partially due to plant development of a root system which is even less able to exploit the limited soil P resources. Development of the magnolioid root structure was proposed as a mechanism by which the plant conserves energy and uses the less costly symbiosis, rather than expending energy to generate roots which may still be unable to acquire adequate P.

Both Hetrick et al. [21] and Price et al. [34] observed that root branching is reduced in infertile soil, increasing dependence on the mycorrhizal symbiosis. In the former study, however, the more elongate, less branched archi-

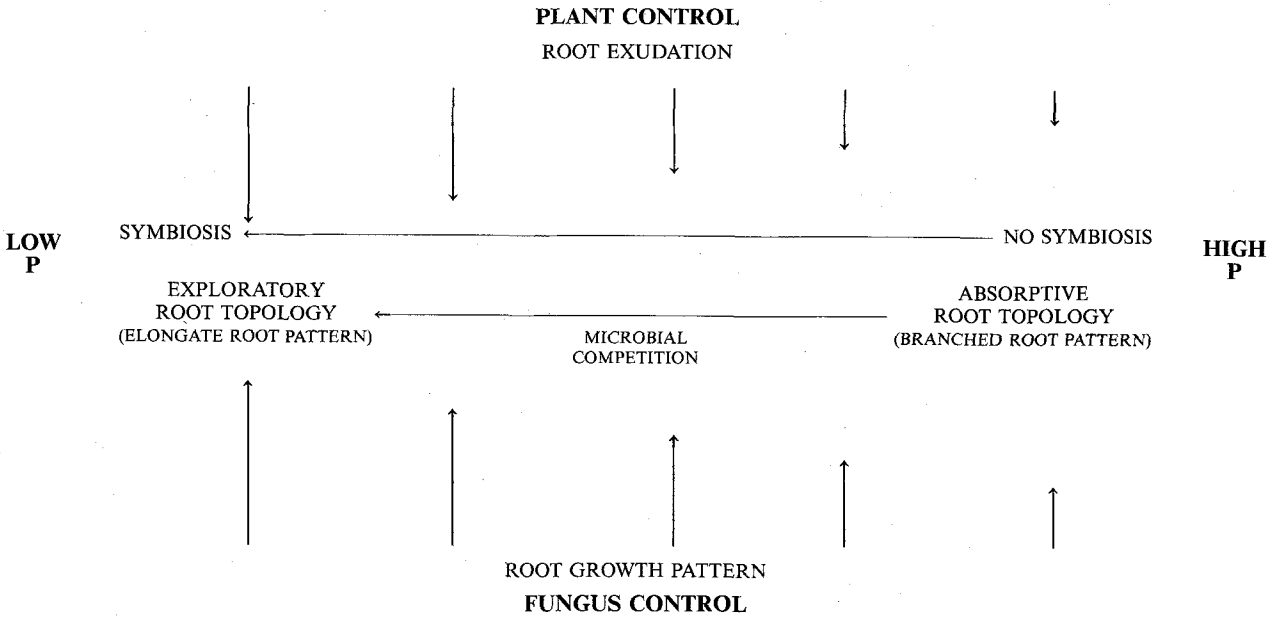

Figure 2. Integrated plant and fungus controls on symbiotic establishment and plant root architecture as influenced by plant dependency on mycorrhizal symbiosis and P availability.

tecture was adopted in response to mycorrhizal symbiosis and was not related to P availability. In the latter study, it was suggested that P fertilization, by increasing rate of root extension and lateral root initiation, would increase root branching, but the effect of mycorrhizas on root branching was not studied directly. Also, the soil P levels compared by Price et al.[34] far exceeded those compared by Hetrick et al.[21]. Therefore, P effects on root branching which were obvious when low and high P conditions (36–75 μg g^{-1}) were compared[34] were not evident within the relatively small range of P conditions (5–35 μg g^{-1}) studied by Hetrick et al.[21]. Considering these two studies together, it appears that high levels of P fertilization can increase branching while mycorrhizal symbiosis decreases branching. A continuum can be envisioned where, at high P levels, mycorrhizal colonization of roots is inhibited and roots are highly branched. As P availability decreases, the root system becomes susceptible to mycorrhizal symbiosis and root branching decreases, increasing dependency on mycorrhizal symbiosis. Once roots are colonized, mycorrhizal fungi may produce hormones or by some other means further decrease root branching and maximize dependence on the symbiosis. In this way, metabolic cost of root production is minimized to the greatest extent possible. Further research will be necessary to confirm or disprove this hypthesis.

Reduced root branching in infertile soils and further reduction in response to mycorrhizal fungi have the same effect of increasing plant dependency on mycorrhizal symbiosis[21, 34]. It is interesting, therefore, to consider whether this effect is limited to mycorrhiza-dependent plants or whether it is shared equally or to a lesser degree by facultative mycotrophs. In recent experiments, Hetrick et al. (unpublished) have demonstrated that the mycorrhizal fungus, *Glomus etunicatum* (Becker & Gerd.) caused similar reductions in branching (increased pathlength) in five highly mycorrhiza-dependent warm-season C_4 grasses indigenous to tallgrass prairie. In contrast, mycorrhizal inoculation did not reduce branching or increase pathlength of the less mycorrhiza-dependent cool-season, C_3 grasses which coexist in tallgrass prairie. Phosphorus fertilization did not significantly alter branching or pathlength in either group of plants. Apparently, the ability of mycorrhizal fungi to increase mycorrhizal dependence by altering root morphology is limited to highly mycorrhiza-dependent plants. Since both warm- and cool-season grasses in this study were colonized by the mycorrhizal fungus (although to different extents), alteration of root architecture by mycorrhizas is probably not simply a function of root colonization but may be more related to differences in plant physiology.

Conclusions

The proposal that VA mycorrhizal fungi mediate changes in root architecture is based upon research involving relatively few plant species and on models which themselves involve assumptions. Further research is clearly needed to determine whether the reported effects of the symbiosis are widespread among plant species. If so, the mechanism by which this mediation occurs should be examined. Hetrick et al.[21] have suggested that hormone production by VA mycorrhizal fungi could alter root architecture, but this hypothesis has not been tested. If hormones produced by mycorrhizal fungi are responsible for

changes observed in root architecture, why would they elicit different responses in highly versus weakly mycorrhiza-dependent plant species? The differential rooting pattern response of obligate and facultative mycotrophs to the symbiosis would imply plant regulation of fungal hormone production or varied sensitivity to hormones produced by the fungi. It might be interesting to test this possibility not only in endomycorrhizal, but also in ectomycorrhizal symbioses, where more information is available already on production and function of plant hormones (see Gogala, this issue).

The model proposed in this review which integrates the effects of phosphorus and mycorrhizal effects on root architecture has not been tested and is simply proposed as a synthesis of existing literature. If plant dependence on mycorrhizal symbiosis is viewed along a continuum, and if mycorrhizal control of root architecture is limited to dependent plant species, a point along the continuum may exist where the capacity of mycorrhizal fungi to alter root morphology switches from a competitive advantage to a disadvantage. This might not be reflected in dry matter measurements or in experiments which examine plants grown in isolation. Therefore, mycorrhizal effects on root architecture should be integrated into our attempts to understand the significance of mycorrhiza for plant competition.

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0014-4754/91/040355-08$1.50 + 0.20/0

Acquisition of nutrients from organic resources by mycorrhizal autotrophic plants

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Summary. Evidence exists to suggest that mycorrhizal fungi are capable of producing enzymes allowing them to access carbon, nitrogen and phosphorus from complex organic resources in soil. This facility is mainly demonstrated in ectomycorrhizal and ericaceous endomycorrhizal fungi associated with highly organic soils and climatically stressed environments. These data support a direct nutrient cycling hypothesis proposed for tropical ectomycorrhizal forests. In terms of forest succession, the evidence agrees with a major contribution of the mycorrhizal symbiosis in late stages of the succession, where elemental cycling becomes increasingly more conservative and process rates limited by biotic factors. Here, tree growth benefits from direct nutrient cycling mediated by their mycorrhizal symbionts.
Key words. Direct cycling; phosphatase; phytase; enzymes; succession; decomposition.

Introduction

Soils are derived from parent rock by the processes of erosion by wind, water, temperature change and the effects of plant roots. Essential plant mineral nutrients are dissolved from the parent material and the whole provides a structural and nutritional resource on which autotrophic plants may survive. Through the fixation of carbon by photosynthesis, carbon is added to the soil in complex forms with mineral nutrients (nitrogen, phosphorus, sulphur, calcium, etc.) as plant litter, either by the shedding of plant parts or in the death of the plant. Soil is the home of many animals (arthropods, nematodes and earthworms) which, together with fungi and bacteria, are involved in the breakdown of these organic resources, using the carbon as an energy source and remobilizing mineral elements into the soil solution. The dead bodies and exudates from these animals also contribute to the organic content of soil. Soil is thus a highly heterogenous medium in which the processes of nutrient immobilization and mineralization occur, resulting in pools of inorganic nutrients in solution which are available for uptake by plant roots[19]. Taking a simplistic view, the role of mycorrhizal fungi is to enhance the plant root's ability to capture dissolved mineral nutrients from the soil solution before they can either be immobilized into tissues of other organisms (fungi, bacteria or competing root systems) or are leached down the soil profile beyond the physical extent of the rooting system. Mycorrhizas are thought to do this by increasing the surface area of the root, thereby extending the nutrient depletion zone further from the root surface (see reviews by Fitter and Hetrick in this issue). A general concept of soil nutrient cycling, as outlined above, is presented in figure 1. In 1968, however, Went and Stark[79] proposed a more direct nutrient cycling system based on their observations of tropical forest soils. They noticed very close associations between ectomycorrhizal roots and their fungal hy-

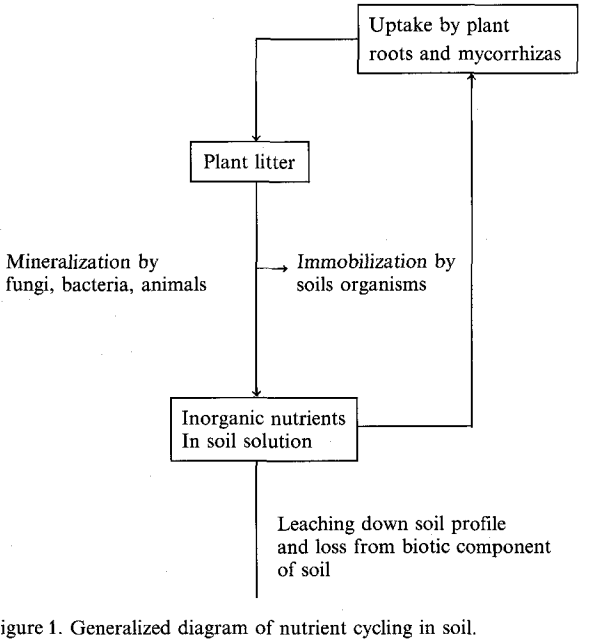

Figure 1. Generalized diagram of nutrient cycling in soil.