Costs and benefits of mycorrhizas: Implications for functioning under natural conditions

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Summary. It is paradoxical that most plants under natural conditions are infected with vesicular-arbuscular mycorrhizal fungi, yet that it is often difficult to demonstrate that infected plants receive any benefit from the association. The costs and benefits of infection are analysed and a hypothesis formulated that infection only yields benefits at times during the life cycle when P demand by the plant exceeds the capacity of the root system. A simulation model is described that suggests that infection density should be more or less constant below a threshold value of root P uptake rate, but that above this value roots should be non-mycorrhizal. More extensive study of mycorrhizas under field conditions is needed to test such predictions.

Key words. Mycorrhizas; cost-benefit analysis; phosphate uptake; field conditions; vesicular-arbuscular mycorrhizas.

The problem

The vesicular-arbuscular mycorrhiza (VAM) is probably the most ancient[27] and widespread[34] symbiosis involving plants. Some of the earliest land plants appear to have had fungi very similar to modern *Glomus* spp. in their roots, and it has been argued that the colonisation of land was only made possible by the development of the association[27]. Current estimates, based on rather unsystematic investigations of around 6,500 species, are that around 2/3 of all extant plant species normally form VAM[34].

Other mycorrhizal associations appear to have evolved since this ancient type and to have become specialised for particular soil types, but the VA mycorrhiza remains the most abundant. It is inconceivable, therefore, that such a persistent symbiosis is neutral: it must either be parasitic or mutualistic, although there is no reason why it should not be both under different circumstances. Law and Lewis[21] show that the lack of speciation in the mycobiont is indicative of a mutualistic rather than a parasitic association, since host reactions to a parasite should result in selection for novel fungal strains, whereas mutualism produces stabilising selective forces.

If the VA mycorrhiza is accepted as a mutualism, the benefits for both partners must outweigh the costs. The cost to the plant and the benefit to the fungus are well defined in terms of carbon, and since the fungus cannot apparently obtain carbon elsewhere, this benefit is absolute. It follows, therefore, that there is no cost to the fungus of the association, though this analysis would not be true for other types of mycorrhiza. The major uncertainty in defining the cost-benefit equation for the symbiosis, is the benefit to the plant. This is most often thought of as increased P uptake, though numerous other possible benefits have been suggested (table 1).

To compare cost and benefit, however, a common currency is required[18], and this is most conveniently carbon. The benefit to the plant must therefore be measured as the increase in net carbon exchange resulting from being mycorrhizal. Assuming that increased P uptake is the primary benefit, a measure of the increase in photosynthetic rate due to a higher leaf P concentration is required. It is known that photosynthetic rate is very susceptible to the inorganic P concentration in the chloroplast[12], that P deficiency causes inhibition of photosynthesis[33] and that, except in the most P-deficient plants, increased P uptake does lead to increased leaf P concentrations. A link between mycorrhizal infection and photosynthetic rate is to be expected, therefore, and has been observed[20].

The question to be posed is whether this cost-benefit equation can be shown to result in net benefit to the plant, which can be translated into increased fitness.

Cost to the plant

That carbon passes from plant to fungus has been unequivocally demonstrated both in laboratory and field culture. Quantitative estimates of this cost suggest that around 10% of that carbon transported to the roots goes to the fungus[3, 17, 20, 32]. Potentially this represents a serious loss of resources to the plant: the concept of resource allocation rests on the principle that the organism has a finite pool of resources and that different end-uses must compete for that pool. Carbon used for mycorrhizal function cannot therefore be used for leaf growth or reproduction.

This carbon loss will, however, not affect the total carbon pool if it can be replaced. There is good evidence that photosynthesis is sink-limited under many circum-

Table 1. Benefits to plants of vesicular-arbuscular mycorrhizal infection. These benefits are listed in descending order of their likely importance.

1. Uptake of poorly mobile nutrient ions:
   certainly phosphate
   probably copper, zinc
   possibly others
2. Improved water relations:
   probably a function of improved P nutrition
3. Protection from soil toxins:
   possibly manganese
4. Protection from fungal pathogens

stances; in other words, its rate is determined by the ability of other organs in the plant to use fixed energy for growth or maintenance[7]. In this case, increased use of fixed carbon by mycorrhizal fungi might simply result in an increased rate of photosynthesis, with no net cost to the plant.

Only, therefore, if photosynthetic rate is in some way controlled by the availability of P within the leaf, will this economic analogy of mycorrhizal functioning apply. In such circumstances, several plant responses may result in improved P supply and so increased photosynthetic rate. These include allocation of more resources to root growth[14], an alteration in the pattern of utilisation of resources within the root, leading to a change in root architecture[8,12], and diversion of photosynthate to mycorrhizal fungi. Which of these produces an optimal response (i.e. greatest contribution to fitness) will depend upon the significance of P limitation in relation to other possible deficiencies and the underlying growth pattern and strategy of the plant. The mycorrhizal option is likely to be particularly effective if P is much more strongly limiting than other factors, since the cost of mycorrhizas is relatively low, while its benefit is predominantly in terms of P; in contrast increased allocation to root growth may be more expensive, but it will yield benefits in terms of other soil resources too.

The relative costs of VAM infection and root growth are hard to determine. Construction costs per unit length are much lower for VAM hyphae than for roots, since hyphae of the external mycelium are typically an order of magnitude finer and hence two orders of magnitude smaller in volume terms, particularly if compared to young, non-vacuolated roots. The internal mycelium may, however, also represent a significant biomass, typically around 5–10% of root biomass, but sometimes higher[10]. Since most of the mycelium is metabolically active, whereas much root material is not, maintenance costs per unit biomass may be as much as an order or magnitude higher for hyphae than for roots. The maintenance cost of the fungal biomass may therefore be comparable to that of the root system in some cases (table 2).

Benefits for the plant

The cost of mycorrhizal infection is a function of the quantity and activity of fungal tissue associated with the roots. That quantity varies widely from plant to plant: some species are non-mycorrhizal, but even those that are habitually mycorrhizal always have more and less heavily infected individuals both within and among populations. If the cost to these individuals varies, it is reasonable to suppose that the benefit varies too.

Numerous explanations are possible for this variation, including those which assume that the translation of increased P uptake into benefit in carbon currency terms varies from plant to plant. I shall assume here, nevertheless, that P uptake is a sufficient measure of benefit.

A relationship between P uptake and the proportion of root tissue infected with fungi can be demonstrated under idealised conditions (fig. 1). Unfortunately, as with much work on mycorrhizas, these idealised conditions – in pots of sterile soil in a growth chamber or glasshouse – are remote from the field soils in which benefits must be obtained. It is rare that such clear relationships between improved plant performance and infection can be obtained under field conditions, except, apparently, under tropical conditions[16]. Although a number of successful applications of VAM inoculation in temperate agriculture and horticulture have been documented[11,25], these are largely confined to specialised systems in which soil sterilisation or micropropagation are standard. After collating data from a large number of field trials in which both changes in yield and in infection density had been reported, McGonigle[22] could find no relationship between the two variables (fig. 2).

Under natural conditions, it is even more difficult to demonstrate that VA mycorrhizal infection benefits plants. The required comparison is between the performances of mycorrhizal and non-mycorrhizal (or more and less mycorrhizal) plants, and this difference can be achieved using fungicides or soil fumigants (table 3). The experiments performed to date show inconsistent results:

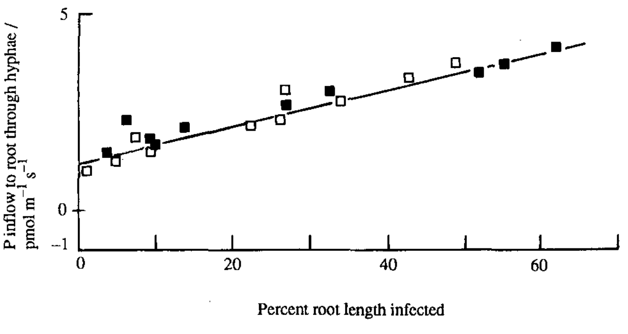

Figure 1. Hyphal contribution to phosphate inflow into onion roots as a function of the degree of mycorrhizal infection. The contribution of the fungal hyphae has been estimated from the difference in inflow between infected and uninfected roots. Plants were infected with *Glomus mosseae* (solid symbols) or *G. macrocarpus* var. *geosporus* (open symbols). Redrawn from Sanders et al.[30]; for other fungi the relationships were different.

Table 2. Costs to plants of vesicular-arbuscular mycorrhizal infection. Data for mycorrhizal fungi are taken from the review by Harris and Paul[10].

Biomass of mycorrhizal fungus	up to 20% of root biomass: take 10% as a typical figure
Cost of growth and maintenance of the mycorrhizal fungus	1–10% of fungal biomass d^{-1} ≡ 0.1–1.0% of root biomass d^{-1}
Root maintenance costs[7]	ca 1.5% root biomass d^{-1}
Therefore cost of mycorrhizal fungus ≈ root maintenance cost	

Table 3. Manipulations of vesicular-arbuscular mycorrhizal infection under field conditions using anti-fungal agents. Table shows whether positive (+), nil (0) or negative (−) effects were reported for levels of VAM infection, plant growth and P concentration in leaf tissue; 'nm' is shown where no measurements were reported.

Technique	System	Effects on infection	Growth	P concn	References
Benomyl	Red clover/arable	−	−	−	5
	Alpine grassland	−/0	nm	+/0	6
	Annuals/dry grassland	0	nm	0	19
	Vulpia ciliata	−	−	0	[a]
	Temperate grassland	−/0	−/0	−/0	23
Rovral	Ruderals/old field	−/0	−/0	nm	9
Methyl bromide	Peas	−	0	−	15
	16 crop species	−	−	nm	28
	Wheat and barley	−	0	nm	28
	6 crop species	−	−	−	36

[a] Carey, P., Watkinson, A. R., and Fitter, A. H., unpublished data

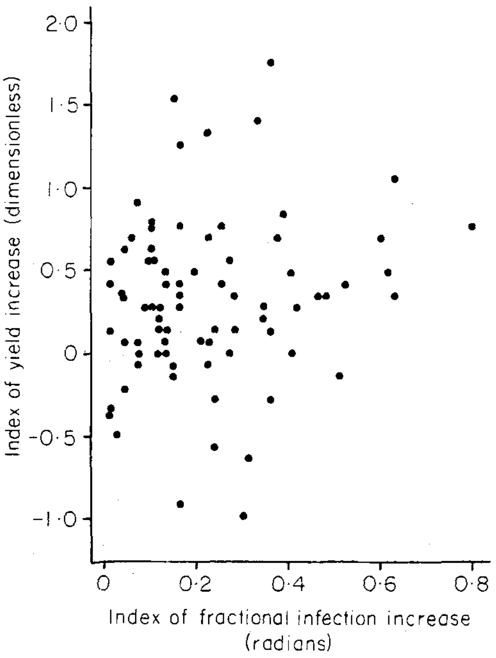

Figure 2. The relationship between an index of yield increase following inoculation with VA mycorrhizal fungi and an index of the consequent increase in fractional infection. Reprinted with permission from McGonigle[22], where details of data sources and calculations are given.

where infection has been reduced (which is not the case for all experiments), there has often but not invariably been a reduction in P uptake or concentration and sometimes a reduction in dry matter production as well.

Part of the problem in measuring such relationships may lie in the difficulty of defining precisely the extent of mycorrhizal infection. VAM infections typically occur as patches within otherwise uninfected lengths of root, and the density and activity of infection in these patches is very variable. Typical measurements of 'percent root length infected' may give a poor indication of the mycorrhizal status of a root system. Even after allowing for such effects, however, these inconsistent results are not surprising. As shown above, infection can only yield benefits if the increased P uptake (or other primary effect) results in net carbon gain. This implies at least that the uptake rate per unit length of mycorrhizal root is greater than could be achieved by the root relying simply on diffusive transport of phosphate ions through soil.

Data on P inflows (uptake rates per unit root length) into plant roots under natural conditions show that they are often very low[23, 24, 31]. For many species growing under natural conditions, it appears that inflow values around 1 pmol m^{-1} root length s^{-1} are typical for much of the growing season. Only one value for the expected inflow of P into an uninfected root system has been published[29]: 3.5 pmol m^{-1} s^{-1} as the 'zero sink' rate for onion roots in a sandy loam soil (i.e. the diffusive rate assuming that phosphate concentration at the root surface had been reduced to zero). Clearly this figure would vary between soils, depending on P buffer power and soil moisture concentration, but it can be taken as an indication of the value that must be exceeded if mycorrhizal transport is to be invoked as a necessary contribution to P inflow.

Such data as are available on P inflows in uncultivated systems (table 4) show that inflows are often much lower than 3.5 pmol m^{-1} s^{-1}; in other words, for many plants for much of the time, the P demand may be so low that there is no need to invoke a mycorrhizal contribution. Yet the fungal biomass will still represent a cost. At any one time, therefore, a manipulative experiment is more likely to find no benefit than a good response to infection.

However, there will be times when P inflows are high enough to require mycorrhizal assistance. In studies on *Holcus lanatus*[24] and cultivated strawberry *Fragaria x ananassa*[4], these peaks of uptake coincided with flowering and fruiting, a period of high P demand. Annuals

Table 4. Measured inflows (pmol m^{-1} s^{-1}) and estimated fluxes (μmol m^{-2} s^{-1}) assuming given values of root radius (μm), for plants grown under field conditions without biocide treatments.

Species	Inflow	Root radius	Flux	References
Pisum sativum	7.8	375	3.3	16
Holcus lanatus	1.4	95	0.7	25
Trifolium repens	1.8	175	4.7	24

must experience such demands each year, but many perennials in uncultivated conditions may not flower so regularly or may regulate the extent of flowering under unfavourable conditions, as shown for shaded stands of *Aster acuminatus*[26]. There are virtually no data on the annual (still less the whole life cycle) P budgets of wild perennials, so that it is impossible to say whether they do experience peaks of P demand which would render mycorrhizal infection essential. Many may use stores of P (or other possibly mycorrhizally-mediated elements) accumulated slowly over previous life cycle stages to fund periods of active growth. Agricultural perennials may have descended from wild ancestors with such conservative strategies, and though the modern plant may have greater P demands, its acquisition system may not have been similarly modified. This is an area which merits much greater study.

If we assume, therefore, that the need for mycorrhizal infection will vary temporally (as well, of course, as spatially), it becomes easier to understand the wide variation in infection density found in plants growing under natural or agricultural conditions. The challenge then becomes the identification of optimum levels of infection in a spatially and temporally variable environment.

A simulation model

There are so many undefined and unmeasured variables in the set of equations that define the costs and benefits of VAM infection, that it may seem premature to construct a simulation model of the system. Yet this is the only effective approach to hypothesis generation, precisely because of these unknowns and the complexity of the interactions between them. The model described here is a simple one that relies on two fundamental relationships describing the benefit in terms of carbon as a currency: one relates the P concentration in leaf tissue to the mean P inflow rate of the root system, and one estimates photosynthetic rate as a function of leaf P concentration. A number of other variables must be supplied. Initially, the total root length of the plant (L_R/m) is set, and the frequency of entry points per m of root (f_{ep}/m^{-1}), so that the number of entry points over the whole root system (N_{ep}) is given by:

$$N_{ep} = f_{ep} \cdot L_R \qquad [1]$$

The mycorrhizal contribution to P uptake depends on the P flux that can be achieved through each entry point (F_{ep}/pmol s^{-1}) and N_{ep}, while the non-mycorrhizal contribution is given by the inflow into uninfected roots (I_R/pmol m^{-1} s^{-1}), so that the mean P inflow for the root system (I_p/pmol m^{-1} s^{-1}) is:

$$I_p = f_{ep} \cdot F_{ep} + I_R \qquad [2]$$

There are no published data relating leaf P concentration to P inflow, but the general form of the relationship between leaf P and P uptake rate is well established. The P concentration in leaves (P_L/mg g^{-1} dry mass) is therefore assumed to be related to I_p by the logarithmic equation:

$$P_L = b \cdot \log_{10} I_p \qquad [3]$$

and in the simulations, a value of 2.0 was used for 'b'. Similarly, photosynthetic rate (ΔC/µmol m^{-2} leaf area s^{-1}) is assumed to be related to leaf P by:

$$\Delta C = c + d \cdot \log_{10} P_L \qquad [4]$$

This relationship, and the values of 4.8 and 6.6 for 'c' and 'd' used in the simulations, were derived by least squares regression from published data[33].

From these relationships, the daily carbon gain (C_{in}) was calculated, assuming a 16-h day and a leaf area: root length ratio (m^2:m) of 1:500.

The carbon cost of mycorrhizal infection is given by:

$$C_{out} = r_m \cdot N_{ep} \cdot L_h \cdot \beta_m \qquad [5]$$

where r_m is the carbon cost of mycorrhizal respiration (including growth; g carbon g^{-1} fungal biomass d^{-1}), L_h is the total length of external and internal hyphae per entry point (taken as 1 m) and β_m is the specific biomass of mycorrhizal hyphae (g m^{-1}). Published values of β_m[2] of $2 \cdot 10^{-6}$ and of r_m[10] of 1.0–1.5 were used.

The optimum mycorrhizal density, defined in terms of entry point number, is then given by obtaining expressions of C_{in} and C_{out} as functions of N_{ep} (fig. 3a), and determining the value of N_{ep} where dC_{in}/dN_{ep} and dC_{out}/dN_{ep} are equal (fig. 3b). If this is done for various values of I_R, which represents the ability of uninfected roots to obtain P and therefore integrates soil P availability and plant P demand, the relationships in figure 4 are discovered.

Simulations have been performed over a range of values of I_R from 0.1 to 10 pmol m^{-1} s^{-1}, which are typical values for field-grown plants[4, 23]. Over a wide range of values of the input variables, the model consistently predicts an optimum entry point density of 1.0 to 1.2 mm^{-1}, which is consistent with many published figures. For example, Wilson[35] recorded a characteristic value of 1.2 entry points mm^{-1} for *Gigaspora decipiens* in *Trifolium subterraneum* roots, irrespective of age of the root system or inoculum density. In the same study, *Glomus fasciculatum* entry point frequency was more variable, ranging from 0.6 to 2.0 in response to the same factors. Soil P supply also affects entry point frequency: in leek[1] f_{ep} declined from 2.7 mm^{-1} at low P to 1.2 mm^{-1} at high P supply, but the proportion of root length infected declined to a greater extent.

The model also predicts that roots should be non-mycorrhizal when P inflow into uninfected roots is greater than 1 – 10 pmol m^{-1} s^{-1}, the exact value depending upon fungal carbon cost and efficiency. The transition from the mycorrhizal to the non-mycorrhizal state should be rapid (fig. 4) once the threshold inflow has been crossed. This suggests that plants should maintain relatively con-

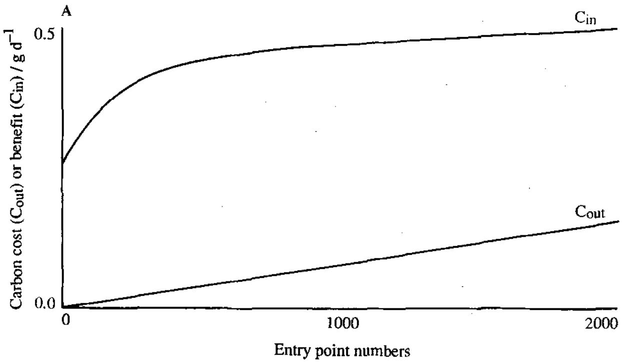

Figure 3a. Relationship between carbon benefit (C_{in}) and carbon cost (C_{out}) and the number of entry points on the root system (N_{ep}). The data were obtained from the simulation model described in the text, with an entry point P flux (F_{ep}) of 0.005 pmol s^{-1} and carbon cost of fungal respiration (r_m) of 1 g g^{-1} d^{-1}.

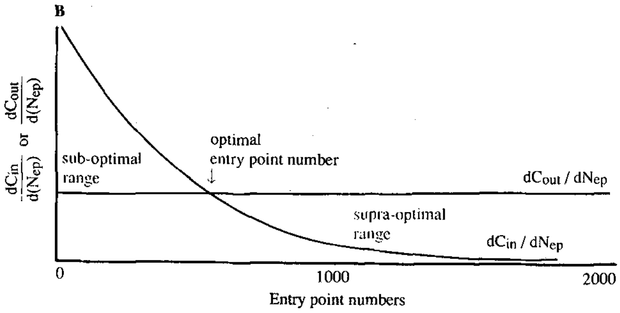

Figure 3b. Derivation of the functions depicted in figure 3a. The optimum number of entry points is where the two curves intersect, i.e.

$$\frac{dC_{in}}{d(N_{ep})} = \frac{dC_{out}}{d(N_{ep})}$$

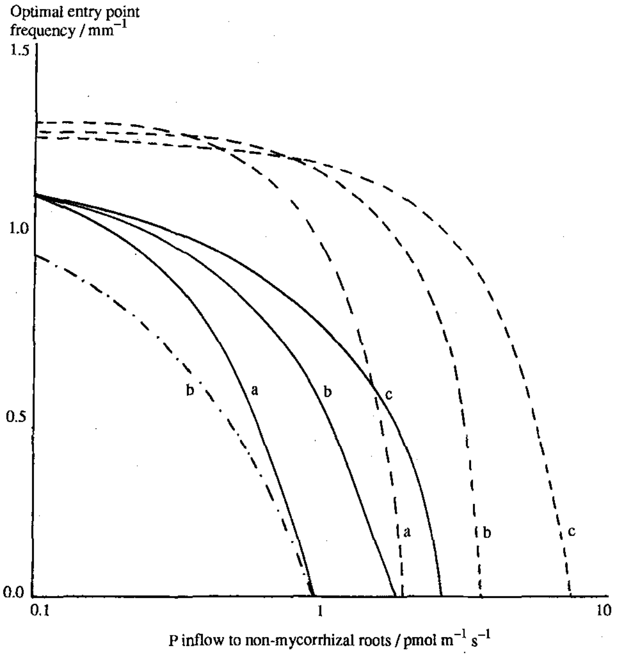

Figure 4. Results of simulations to determine optimum entry point frequency (f_{ep}) at different values of root P inflow, which will be related to soil P availability. Other variables are carbon cost of fungal respiration (r_m, g g^{-1} d^{-1}) and P flux per entry point (F_{ep}, pmol s^{-1}).

- - - - - $r_m = 0.5$	a $F_{ep} = 0.002$
——— $r_m = 1.0$	b $F_{ep} = 0.005$
-·-·-·- $r_m = 1.5$	c $F_{ep} = 0.010$

stant levels of infection in their root systems, irrespective of soil P availability, unless that is so high as to render infection of no value. This is consistent with many observations that particular species tend to be characteristically heavily or lightly infected in a wide range of habitats. The wide variation between species could then be explained in terms of the inflow rates that their root systems are capable of maintaining.

Other simulations, the results of which are not shown here, demonstrated that the predictions are quite insensitive to the length of root system, since this does not (in this model) alter f_{ep}. Equally, altering the hyphal length associated with each entry point has the same effect as altering the P flux per entry point.

This model is not intended to offer a faithful representation of the functioning of vesicular-arbuscular mycorrhizas, but rather to indicate the variables to which the system should be sensitive. It offers a number of testable predictions about VAM function, for example that entry point frequency should be relatively constant over a wide range of soil P availability. Most importantly, reliable data on P inflows are needed and these must be related to levels of VAM infection, preferably measured in terms of entry point density, infection units or fungal biomass. Some progress has been made in this direction already[28], but more mycorrhizologists must be willing to forsake the safety of the laboratory for the excitement of the field if developments are to continue.

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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.