Mycorrhiza (1992) 1:47–53

Mycorrhiza

Original papers

Interactions between plants: the role of mycorrhizae

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Summary. We present and discuss evidence, mostly from our own research, on some possible roles of mycorrhizae in interactions between plants. Experiments investigating whether seedlings become more rapidly infected with mycorrhiza if they are near large, already infected plants have shown that contact between the seedling's roots and established mycelium sometimes speeds up infection but on other occasions it does not. The reason for the discrepancies is not clear. Mycorrhiza can substantially alter the balance between competing plant species in a way that would not be predicted from their response when growing separately. An experiment involving large and small plants of the same species growing together showed little effect of mycorrhiza on the balance between plants of different sizes. The rate of transfer of ^{32}P between plants of *Lolium perenne* or *Plantago lanceolata* was so slow, even when they were mycorrhizal, that phosphorus transfer between living plants seems unlikely to be of major ecological importance. However, nitrogen was found to be transferred much more freely than phosphorus between *P. lanceolata* plants. Situations are discussed in which there could be a source-sink relationship between plants causing net flow of carbon or mineral nutrients from one to the other. If nutrients pass from dying roots to living plants via mycorrhizal links, this could result in preferential nutrient cycling between species that share the same type of mycorrhiza. Some evidence is presented that this does happen.

Key words: Competition – Grassland – Nutrient transfer – Nutrient cycling – Seedling establishment

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Introduction

Up to now much of the research on the influence of mycorrhizae has involved experiments with individual plants in pots. In the real world outdoors, plants usually grow close together, in populations of a single species or in many-species communities; these may be even-aged, or mixed-age with seedlings establishing close to large plants. Often the roots of a plant intermingle with those of its neighbours. Plants may influence each other, for example by competition, nutrient cycling or by acting as a source of fungal inoculum. The aim of this paper is to consider some roles that mycorrhizae can play in such populations and communities, roles that would not be detected when studying a single isolated plant. In other words, we consider how mycorrhizae are involved in interactions between plants. This paper is not a comprehensive review: it concentrates on a few aspects and uses evidence mainly from our own recent research; published results by other workers are mentioned more briefly when relevant.

Some of the ways in which mycorrhizae could alter interactions between plants involve the formation of mycorrhizal links. It has been known for more than a decade (Heap and Newman 1980) that when the roots of two plants, even plants of different species, are infected by the same mycorrhizal fungus, hyphae can link the internal infection in the two plants. Links have so far been reported between a few ectomycorrhizal species and between a few vesicular-arbuscular mycorrhizal (VAM) species (Read et al. 1985; see Newman 1988 for a list of species and references). Fowles and Newman (unpublished work) have more recently obtained photographs showing VAM links between a clover and a grass, *Trifolium pratense* and *Lolium perenne*.

Infection of seedlings

In most experiments on mycorrhiza, the mycorrhizal plants become infected from spores or infected dead roots. In the field most seedlings establish close to ex-

isting plants and another method of infection is thus possible: the roots of the seedling may grow into contact with external mycorrhizal hyphae connected to roots of older plants. Although this seems likely to be important in many field situations there is so far very little supporting evidence. If infection does occur first by this direct contact method, before infection from spores or dead roots, then we might expect that seedlings growing close to larger plants would become infected more quickly than seedlings in the same soil without the large plants. We now describe three experiments which investigated this possibility.

Eissenstat and Newman (1990) grew *Plantago lanceolata* in a sandy soil from old dune grassland. The soil was heat-sterilized and then reinoculated with mixed root material from the dune grassland. When the plants sown initially (called 'large plants') were 2 months old, further root inoculum was mixed into the soil and two seedlings of the same species were planted adjacent to the large plants. Other containers were treated in the same way (including inoculation on both dates), except that no plant was put in on the first occasion and the seedlings thus grew without any large plant. Table 1a shows the amount of VA-mycorrhizal infection 5 weeks after the seedlings were planted. The seedlings had a similar amount of infection to the large plants when the two grew together, but seedlings growing alone had less infection; thus the presence of an already infected plant did speed up infection.

Jasper et al. (1989) grew VAM-infected *Trifolium subterraneum* for 6 weeks and then sowed in seedlings of the same species. By using a mesh they were able to arrange for the seedling's roots to be (a) among the roots of a large plant, (b) among VAM hyphae attached to a large plant (though separated from that plant's roots), or (c) among roots of a large plant whose shoot had recently been removed. Table 1b shows that infection in the seedlings was least if they were close to living roots of the established plants, and much greater if they were near detached roots. This result is almost exactly the opposite of the results for *Plantago* in Table 1a.

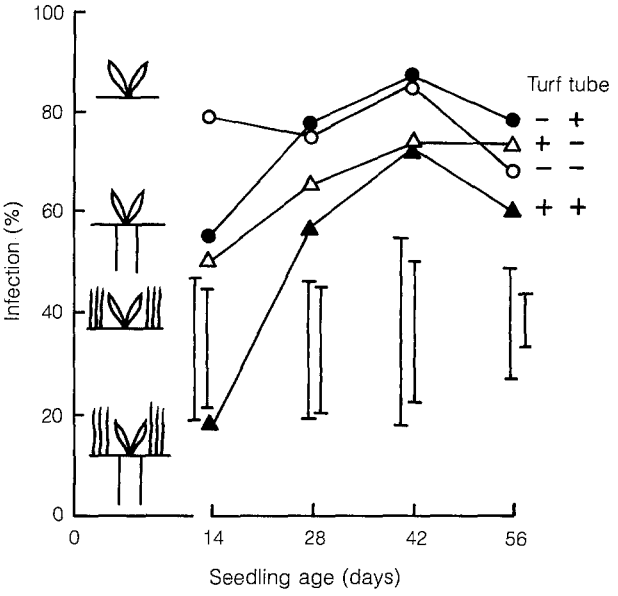

Fig. 1. Vesicular-arbuscular mycorrhizal (VAM) infection (percent root length infected) in seedlings of *Plantago lanceolata* planted on day 0 into grass sward or bare plots, with or without below-ground tubes (turf, tube). The treatments are indicated by the drawings on the left and the symbols on the right. The *vertical bars* show least significant differences at $P=0.05$; the *left bar* of each pair is for comparison between turf categories, the *right bar* for comparison within the same turf category

Table 1. Effect of a large plant on the amount of vesicular-arbuscular mycorrhizal (VAM) infection in seedlings of the same species. Numbers are percent root length infected. * Difference significant at $P<0.05$; NS, not significant

(a) *Plantago lanceolata*. Experiment of Eissenstat and Newman (1990)

	Infection in	
	Seedlings	Large plant
Large plant present	20.0 NS *	23.4
Large plant absent	9.4	

(b) *Trifolium subterraneum*. Experiment of Jasper et al. (1989)

	Infection in seedling at age	
	2 weeks	4 weeks
Seedling's roots in contact with		
Living roots of large plant	14 *	2 *
Hyphae attached to large plant	46 *	59 NS
Roots of large plant (shoot detached)	71	52

One possible explanation for the discrepancy between these two sets of results is that large plants can have two effects, shading by the shoots slowing mycorrhizal infection but contact between roots increasing it. A field experiment by one of us (Ramos 1987) attempted to investigate the separate effects of shoot and root on the rate of mycorrhizal infection. The experiment was conducted in grassland near Bristol, England. In four replicate plots the vegetation was cleared by repeated clipping. In these and in four plots with vegetation, soil columns 15 cm deep × 4 cm diameter were removed at numerous locations. Plastic tubes 4 cm in diameter were inserted into half of the holes; then all the holes were refilled with the soil. One month later, in August, a seedling of *P. lanceolata* was planted into each position. Thus there were four treatments: in the presence or absence of the grassy sward, each with or without the tube. In the grassy plots the tubes prevented intermingling of the roots of the plantain seedlings and the other plants; the rims of the tubes were level with the soil surface. Seedlings were harvested every 2 weeks and the percentage root length infected by

VAM was determined. Figure 1 shows that from 4 weeks onwards infection stabilized at about 60%–80% in all treatments, but the rate at which this plateau infection was achieved differed between treatments. Among seedlings growing in the turf, those whose roots could intermingle with the established plants had significantly greater infection at 2 weeks than those whose roots were within the tube, suggesting that contact with mycelium attached to living roots contributed to the infection process. However, infection was even faster in the bare areas where there was no living root. Lack of shading of the seedlings could have been involved, but there are reasons to think that this is not the full explanation. Firstly, in a glasshouse experiment (Ramos 1987), shading that was sufficient to markedly reduce the growth of *P. lanceolata* had very little effect on the rate of mycorrhizal colonization. Secondly, in Fig. 1 there is a difference at 2 weeks between the seedlings with and without tubes in the bare plots. Although this was only just statistically significant, it suggests that the tubes may have affected the rate of infection in some other way besides preventing root contact.

These three experiments provide evidence that close proximity between the roots of a seedling and roots of an established, infected plant can sometimes speed up VAM infection in the seedling. However, the results of the three experiments do not entirely agree, for reasons that are not clear to us, and this matter deserves further research.

Competition between plants

When competition between plants for nutrients is discussed, it is often in terms of the roots drawing nutrients from a common pool in the soil. If the plants are mycorrhizal then we also need to consider the ability of their external mycelium to capture nutrients. Furthermore, if the plants share a common external mycelium, then competition exists between the plants to acquire nutrients from that mycelium. We have no definite information on which characteristics, anatomical or physiological, would allow one plant to acquire more of a nutrient element from a mycorrhizal fungus than its neighbour. We confine ourselves here to asking two questions about the influence of mycorrhiza on the balance between competing plants: (1) Can mycorrhizal infection alter the balance between species? (2) Can it alter the balance between large and small plants?

Grime et al. (1987) grew the grass *Festuca ovina* in trays of nutrient-poor sand with or without VAM. Seeds of 20 British grassland species (some grasses, some dicotyledons) were then sown into each tray. *F. ovina* grew less well in the mycorrhizal trays compared to the non-mycorrhizal trays; seedlings of many of the other species grew substantially better, notable exceptions being two non-mycotrophic species. This experiment provides evidence that VAM may be important in allowing coexistence of species in grassland, thus helping to maintain diversity. However, the results leave unclear whether the seedlings grew better (1) because mycorrhizae favour small plants against large plants when they grow together, or (2) because mycorrhizae increase the growth of some species but not others. In favour of the latter explanation, we note from these results that all the seedlings most favoured by VAM were dicotyledonous, and that seedlings of *F. ovina* were reduced by VAM almost to the same extent as were the larger *F. ovina* plants. In order to distinguish between these two possible effects of mycorrhiza on competition, it is necessary to investigate separately the effect of mycorrhizas on (1) the balance between different species of the same age, and (2) the balance between plants of the same species but of different ages. We describe here an experiment of each sort. A few experiments of type 1 have been reported previously (Fitter 1977; Hall 1978).

Ramos (1987) grew *L. perenne* and *P. lanceolata* in a glasshouse in pots of heat-sterilized, nutrient-poor, grassland soil that was initially mycorrhiza-free. Two seedlings were planted into each pot, either two *L. perenne*, two *P. lanceolata* or one of each. After 3 months, when it was clear from the size of the plants that they were competing, half of the pots were inoculated with VAM-containing root material. In this way we ensured that the effects of VAM only occurred during a period when the plants were interacting strongly. After a further month, mycorrhizal infection had become established in the inoculated pots. Growth over the following 3 months (age 4–7 months) was determined by destructive harvests of the shoots and is expressed as relative growth rate (RGR) in Fig. 2. The standard error bars are quite wide, but the pattern is clear. When the two species were separate they had similar relative growth rates; this is true both when they were mycorrhizal and non-mycorrhizal. Therefore, one might expect that they would be well balanced in competition

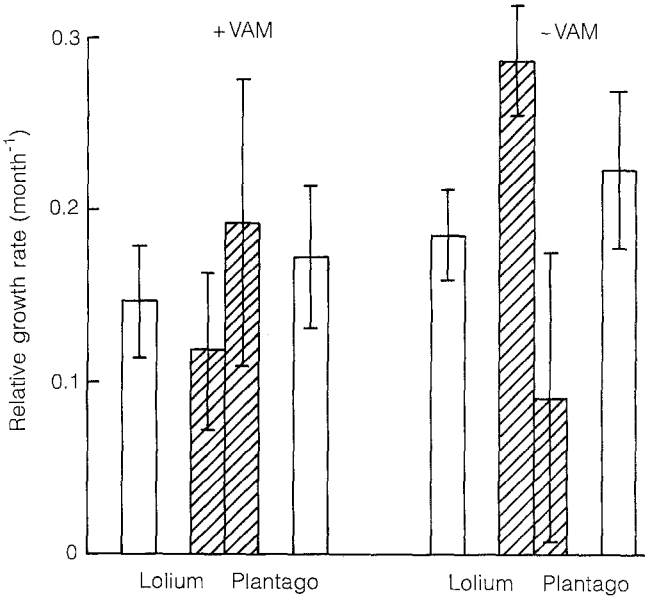

Fig. 2. Relative growth rates of *Lolium perenne* and *Plantago lanceolata* growing separately (*open bars*) or together (*hatched bars*), either VAM-infected or not. *Vertical lines* show standard errors

Table 2. Dry weight (mg) of shoots of *Plantago lanceolata* seedlings in experiment of Eissenstat and Newman (1990). * Difference significant ($P<0.05$); NS, not significant

	−VAM		+VAM	Mean
Large plant present	18.1		28.3	23.2 *
Large plant absent	29.0		37.8	33.4
Mean	23.6	*	33.1	
Ratio $\left(\frac{\text{large plant present}}{\text{large plant absent}}\right)$	0.62	NS	0.75	

and that their competitive balance would be little affected by mycorrhiza; this was not the case. When the two species were in the same pot and were mycorrhizal, *Plantago* had the higher mean RGR but the difference between the species was not statistically significant. In the non-mycorrhizal two-species pots, *Plantago* grew poorly and significantly more slowly than *Lolium*. This suggests that the ability of *P. lanceolata* to coexist with *L. perenne*, as it does in many British grasslands, is dependent on mycorrhiza. This conclusion would not have been reached if we had only studied the two species growing separately. Taking into account the fact that these two species form mycorrhizal links when growing in this soil (Heap and Newman 1980), the results suggest that *P. lanceolata* roots on their own compete poorly against *L. perenne* roots for nutrients from the soil pool, but compete successfully for nutrients from a common mycorrhizal mycelium. Evidence that competition for phosphorus was important in this experiment comes from another experiment (Ramos 1987) in which the same species were grown together on the same soil, with or without VAM infection, and then ^{32}P was applied to the soil. The relative amounts of ^{32}P acquired by the plants closely paralleled the hatched bars in Fig. 2.

The experiment by Eissenstat and Newman (1990) mentioned earlier, involving large and small *P. lanceolata* plants, provides information on whether mycorrhizae alter the balance between large and small plants. In addition to the mycorrhizal containers previously described, others were treated in the same way except that they were not inoculated and remained non-mycorrhizal. Table 2 shows the shoot dry weight of the seedlings when 5 weeks old. Mycorrhizal infection increased seedling growth. The presence of a large plant reduced the growth. However, there was no significant interaction between the two factors: the ratios on the bottom line of Table 2 suggest a slightly greater competitive effect by the large plant in the non-mycorrhizal than the mycorrhizal pots, but this was not statistically significant ($P>0.2$ by analysis of variance with log transformation). So mycorrhizae appear to have had little effect on the competitive balance between large and small plants in this experiment, even though the large plants accelerated mycorrhizal infection in the small plants (Table 1a).

Transfer of substances between plants

Transfer between living plants

The substances whose transfer between plants has attracted most attention are mineral elements, in particular their transfer from dying to living plants, in other words nutrient cycling. The discovery of mycorrhizal links between plants has increased interest in the possibility of nutrient transfer between living plants. It also raises the possibility of transfer of organic materials, for example, from an established plant to a seedling growing in its shade. Read and co-workers (1985) have shown that ^{14}C can be transported between plants by mycorrhizal links, either VAM or ectomycorrhizal. However, it is not yet known whether there is a net transfer of carbon sufficient to influence the growth or survival of the 'receiver' plant. This topic has been reviewed elsewhere (Newman 1988). Here we concentrate on transfer of phosphorus and nitrogen.

Several experiments have shown that ^{15}N or ^{32}P fed to one plant can later be found in a neighbouring plant, and that the transfer is substantially increased if the plants are mycorrhizal (Newman 1988). Eason (1987) carried out an experiment designed to investigate how important interplant transfer of phosphorus may be in grassland. A field of grass may be considered to be made up of many tillers (branches); some tillers belong to the same plant and so have direct anatomical connection, others belong to different plants but their roots may be connected by mycorrhizal links. The aim was to compare the rate of ^{32}P transfer between tillers on the same grass plant with the rates between plants, either mycorrhizal or not. *L. perenne* was grown in phosphorus-deficient pasture soil, two plants per pot, either VAM-infected or not. The plants were grown until the root density was similar to that in the pasture from which the soil had been taken (where *L. perenne* is abundant). Then carrier-free ^{32}P was fed to one randomly chosen tiller of one plant in each pot by immersing cut leaf tips for 48 h in a solution of the isotope. More than half of the ^{32}P moved out of the fed tiller into other parts of the same plant within 7 weeks (Table 3). However, as there were more than 10 tillers per plant, the concentration of ^{32}P was still about 10 times as high in the fed tiller as in the rest of the plant. Equil-

Table 3. Distribution of ^{32}P in shoot material of *Lolium perenne*, 7 weeks after ^{32}P was fed to one tiller on one of the two plants in each pot

	Percent[a] of ^{32}P		Concentration of ^{32}P (cpm/dry weight)	
	+VAM	−VAM	+VAM	−VAM
In fed tiller	38.0	47.3	2848	2571
In remainder of fed plant	59.2	51.7	267	236
In other plant	2.8	1.0	13.7	4.9

[a] Percent of total amount of ^{32}P in shoots of both plants

ibration within the plant is evidently slow. Transfer of ^{32}P between plants was about 3 times as fast if the plants were mycorrhizal, in agreement with previous results (Newman 1988). But even if the plants were mycorrhizal, the rate of transfer between plants was only about one-twentieth the rate within plants. Another way to consider these results is to estimate the rate of progress towards equilibrium. If we assume that the rate of ^{32}P transfer (and by implication total phosphorus transfer) between tillers or plants is proportional to the difference in concentration, then the concentration in each tiller or plant should decay exponentially towards equilibrium. From the results in Table 3, we can calculate the half-times for equilibration, i.e. the time taken for the concentration to reach the mid-point between its initial and final (equilibrium) values. The half-time for equilibration among tillers within a single plant is approximately 1–2 months. For equilibration between plants, it is approximately 2 years if the plants are mycorrhizal, approximately 6 years if they are not. These times may be compared with the longevity or rates of turnover of individual leaves and tillers on British perennial grasses: the half-lives of individual leaves are commonly a few months, and of tillers approximately 1 year or less (Langer 1956; Sydes 1984). This suggests that phosphorus movement between tillers on a plant can be fast enough to make a contribution to the phosphorus content of a developing tiller but that phosphorus movement between plants, even if linked by mycorrhizal hyphae, is unlikely to make much contribution, since it is slow relative to the life-span of tillers.

It should not be assumed that all elements are transferred between plants as slowly as phosphorus. Eissenstat (1990) compared the rates of nitrogen and phosphorus transfer between two *P. lanceolata* plants. The plants were grown with split root systems; some of the roots intermingled but each plant had some roots in a separate volume of soil so that it could be fed an isotope. All the plants were VA-mycorrhizal. At age 4 months, one plant of each pair was fed ^{15}N and ^{32}P. The increase in total nitrogen and phosphorus in the shoot of the other ('receiver') plant was estimated during a 19-day period following labelling. Using measurements of the ^{15}N and ^{32}P content of the shoots of the receiver plants, it was possible to calculate how much of this increase in nitrogen and phosphorus was by transfer from the 'donor' plant and how much was by uptake from the soil by the receiver's roots. 'Transfer' here is not necessarily confined to transfer via mycorrhizal links; it would include any nutrients lost from donor plants to the soil and then taken up by receiver plants. Figure 3 shows that this increase in phosphorus was almost entirely by uptake from soil: the transfer component (black portion) was very small. In contrast, nitrogen transfer made a substantial contribution. (The two treatments will be discussed later.) This suggests that nitrogen may move much more freely between mycorrhizal plants than does phosphorus. This has important implications for nitrogen transfer from legumes to non-legumes. Although mycorrhizas have been shown

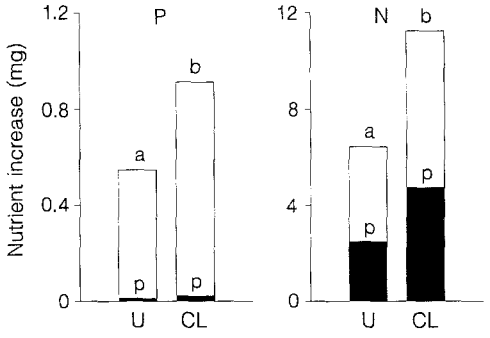

Fig. 3. Increase in phosphorus (*P*) and nitrogen (*N*) in shoot of 'receiver' *Plantago lanceolata* during 19 days after shoot of neighbouring 'donor' plant had been clipped (*CL*) or not (*U*). *Black portion of bar* is amount estimated to have been transferred from donor; *open portion* is estimated uptake from soil. For each element, *bars* bearing different letters are significantly different ($P=0.05$). From Eissenstat (1990)

to increase ^{15}N transfer between plants, it has yet to be shown that they contribute substantially to the transfer of nitrogen from legumes to non-legumes (Haystead et al. 1988).

The experiments we have described in this section have relied on the use of the isotopes ^{15}N and ^{32}P. Movement of an isotope does not prove that net transfer of that element has occurred. Experiments with plants growing in solution culture have shown that roots actively taking up nitrogen and phosphorus can at the same time lose these same elements to the external solution, though usually at a slower rate (Morgan et al. 1973; Elliott et al. 1984). Thus we may expect that if a plant growing in soil is fed through its shoot with ^{15}N or ^{32}P some of the isotope will be lost to the soil and a proportion of this will then be taken up by intermingling roots of neighbouring plants. Thus the isotope will reach another plant even if the net movement of nitrogen and phosphorus is from the soil into both plants. For genuine net transfer of an element from one plant to another to occur there needs to be a source-sink relationship, i.e. some sort of driving force to cause the net movement. There could be a strong source-sink relationship for carbon between a large plant growing in full light and a seedling shaded by it. It is possible that plants might have substantially different mineral nutrient status, even when their roots intermingle. Legumes and non-legumes provide one example. Nitrogen and phosphorus concentrations in roots can also differ between non-legumes, as shown by work of Gay et al. (1982). They analysed the roots of plants growing in chalk grassland in England at various times of year and also examined them for mycorrhizal infection. Table 4 shows their data for plants collected at one site in March 1980 and 1981. Nitrogen and phosphorus concentrations in the roots differed several-fold between the species. The non-mycorrhizal species had the highest concentrations; they tended to grow in disturbed microsites. The annual and biennial mycorrhizal species tended to have higher concentrations than the perennials, a warning against assuming that larger established plants will necessarily be the 'donors' to smaller

Table 4. Concentrations (mg g^{-1}) of nitrogen and phosphorus in roots of species collected from chalk grassland at Devil's Ditch, England in March; data of Gay et al. (1982)

			Nitrogen	Phosphorus
Arenaria serpyllifolia	Annual	NM[a]	18	3.1
Myosotis arvensis	Biennial	NM	24	2.5
Blackstonia perfoliata	Annual	VAM	14	0.9
Gentianella amarella	Biennial	VAM	ND[b]	1.3
Verbascum nigrum	Biennial	VAM	7	1.5
Sanguisorba minor	Perennial	VAM	9	0.6
Festuca ovina	Perennial	VAM	9	0.4
Carex flacca	Perennial	VAM	4	0.3

[a] Non-mycorrhizal
[b] Not determined

plants if transfer of nutrients occurs. In the experiment of Eissenstat and Newman (1990) described earlier, the concentrations of nitrogen and phosphorus in the shoots were higher in the seedlings than in the older plants, whether they were mycorrhizal or not. Nutrient concentrations in whole shoot or root systems are only a crude indication of a source-sink relationship, which may be more closely related to concentrations in particular cells, particular parts of cells or to particular compounds.

Another possible cause of a source-sink relationship is selective grazing of some plants. Repeated clipping of the shoots of *L. perenne* causes substantial loss of ^{32}P from the roots (Eason and Newman 1990). In one treatment of the experiment on nitrogen and phosphorus transfer between *P. lanceolata* mentioned above (Eissenstat 1990), all the leaves of the donor plants were cut off near the base soon after the isotopes had been fed; other plants were left unclipped. The increase of both nitrogen and phosphorus in the receiver plants was significantly greater if their partner donor plant had been clipped (Fig. 3). However, the increased phosphorus acquisition was almost entirely by increased uptake from soil; transfer of phosphorus between plants remained very small. How much of this increased uptake was via mycorrhizal fungi is unknown. The results for nitrogen are less clear-cut. The black bar in Fig. 3 is larger for nitrogen transfer from clipped than from unclipped plants, which suggests that part of the increased nitrogen acquisition by the receiver plant was by transfer. However, the difference between treatments is not statistically significant and no definite conclusion can be drawn.

Nutrient cycling from dying roots

In this final section we consider the role of mycorrhiza in a more conventional transfer of nutrients, from dying plant parts to living plants. If the shoots of *L. perenne* plants are detached, a substantial proportion of the phosphorus in the roots is lost within 3 weeks, even if the plants were grown under nutrient-deficient conditions (Eason and Newman 1990). The results of ^{32}P transfer studies (Ritz and Newman 1985) indicate that part of this released phosphorus can be captured by another, living plant if its roots intermingle with the dying roots, and that the amount captured is increased several-fold if the dying and living roots are linked by mycorrhizal fungus. This does not in itself prove that transfer between dying and living roots occurs via mycorrhizal hyphae: an alternative would be that the mycelium attached to the living plant increases its ability to capture nutrients released from the dying roots into the soil. Here we concentrate on one hypothesis that arises if transfer of phosphorus between dying and living roots does occur through hyphal links. In some plant communities species grow together which have different types of mycorrhiza; examples are VAM and ectomycorrhizal species in some forests and in savannas, VAM and ericoid species in heathland. If there is nutrient cycling between plants via mycorrhizal hyphae, we should expect preferential cycling between species that share the same type of mycorrhiza. We have tested this in pot experiments (Eason and Newman, in press).

Each pot initially contained three plants. The soil was unsterilized and each plant formed its normal type of mycorrhiza. The combinations were:

Fraxinus excelsior (VAM), *L. perenne* (VAM), *Acer pseudoplatanus* (VAM);

F. excelsior (VAM), *L. perenne* (VAM), *Larix eurolepis* (ECM, ectomycorrhizal);

A. pseudoplatanus (VAM), *L. perenne* (VAM), *L. eurolepis* (ECM);

Calluna vulgaris (ERM, ericoid mycorrhizal), *C. vulgaris* (ERM), *Molinia caerulea* (VAM).

The three plants were placed in a row, in the order listed, with the central one as 'donor'. Thus in the first combination listed both 'receivers' had the same type of mycorrhiza as the donor, but in the other three combinations one of the donors was of a different type (and incapable of forming mycorrhizal links). In some pots, ^{32}P was fed to the shoot of the donor plant and after a few days to allow its roots to become labelled its shoot was cut off and removed. In the remaining pots, the shoot of the central plant was also removed, but ^{32}P was supplied by injecting it into the soil. The amount of ^{32}P in the shoots of the two remaining plants was later determined. Thus we studied competition between the two remaining plants to acquire phosphorus either from the soil pool or from dying roots.

In the top combination shown in Fig. 4, where all three species were VAM, the distribution of ^{32}P between *Fraxinus* and *Acer* was virtually the same whether the ^{32}P had been supplied to the soil directly or via *Lolium* roots. In the next example, *Fraxinus* and *Larix* were about equally effective at acquiring ^{32}P from soil, but *Fraxinus* (which was VAM) was more effective at acquiring it from the dying roots of *Lolium* (also VAM). In both the other examples, the species that had the same type of mycorrhiza as the donor also acquired a higher proportion of the ^{32}P when the isotope was pro-

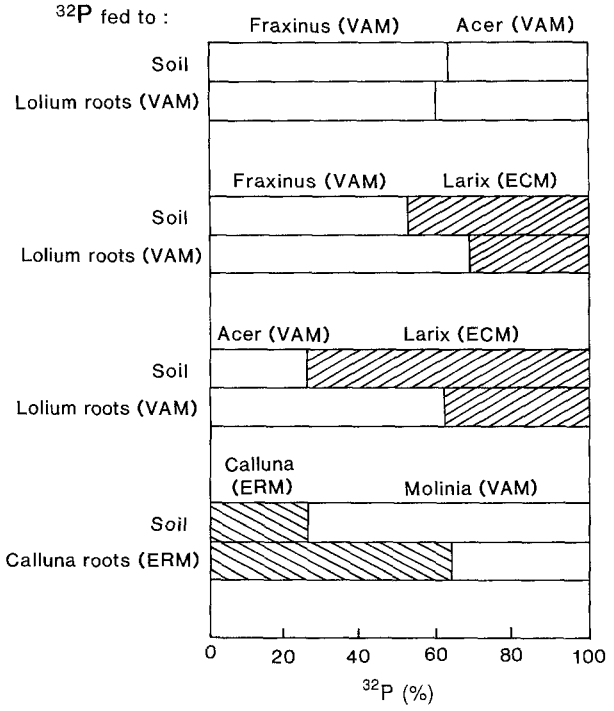

Fig. 4. Distribution of ^{32}P between shoots of two 'receiver' plants after ^{32}P was either injected into the soil or fed to the shoot of a third plant growing between them. For further details see text. The *hatching* is used to distinguish plants with different types of mycorrhiza

vided via the donor than it did when it was provided direct to the soil. These results are in agreement with the hypotheses that phosphorus can be transferred from dying roots to living plants by mycorrhizal links, and that this results in preferential cycling of nutrients between species that have the same type of mycorrhizal infection. We do not regard the evidence as by any means conclusive: no non-mycorrhizal controls were included to indicate whether mycorrhizae were really involved, nor do we have definite evidence that mycorrhizal links between the plants were formed. Nevertheless, this is initial evidence for preferential nutrient cycling between certain species which could, if it proves to be widespread, have an important influence on the structure and composition of plant communities.

Conclusion

This paper has been selective in its choice of topics. Of the possible roles of mycorrhizae in populations and communities that we have discussed, three appear to be important on the basis of the limited evidence we have presented and to deserve further investigation.

1. Mycorrhizal infection can substantially alter the balance between competing species, but we do not know how widespread this is or the mechanisms involved.

2. Transfer of phosphorus between living plants via mycorrhizal links may be too slow to be of much ecological significance, but there is some evidence that nitrogen can be much more rapidly transferred, and this could be important in transfer from legumes to non-legumes.

3. There is preliminary evidence that where plant species with different types of mycorrhiza grow together there can be preferential cycling of phosphorus between plants with the same type of mycorrhiza.

Acknowledgements. Research described here was made possible by financial support from the Natural Environment Research Council (UK), the Ministry of Agriculture, Fisheries and Food (UK), the National Science Foundation (USA) and the Gulbenkian Foundation (Portugal).

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