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Effects of mycorrhizal fungi on plant populations

Roger T. Koide[1,3] & Ian A. Dickie[1,2]
[1]*Department of Horticulture, The Pennsylvania State University, University Park, PA 16802 USA;* [2]*Current address: Department of Forest Resources, 115 Green Hall, 1530 N. Cleveland Ave., St. Paul, MN 55108, USA;* [3]*Corresponding author**

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Abstract

We discuss four potentially important interactions between mycorrhizal fungi and populations of plants. First, vesicular-arbuscular mycorrhizal colonization has been shown to increase reproduction (via both male and female functions) and offspring survival, and thus it can increase population size, at least in the short term. This is undoubtedly important to wild plant species and especially to those whose success depends on high rates of reproduction such as early successional annuals. Second, the positive response in growth and reproduction to vesicular-arbuscular mycorrhizal colonization may be inversely related to plant population density. All else being equal, this would tend to stabilize the density of natural plant populations over time. It may also explain why positive responses to mycorrhizal inoculation of dense crops are rare. Third, vesicular-arbuscular mycorrhizal fungi can increase inequality in size and reproduction among plants within a population. Mycorrhizal fungi may thus exaggerate the genetic overrepresentation in the next generation of the most robust individuals in the current generation. Fourth, established mycorrhizal plants may serve as important sources of inoculum for initially non-mycorrhizal, conspecific seedlings. This may affect regeneration, and could contribute to patchy distributions of species within the community.

Introduction

A great deal of research has been conducted to determine the effects of mycorrhizal fungi on individual host plants. Much has been learned about the mycorrhizal symbiosis and much will continue to be learned by studying individual plants, particularly about the genetics, biochemistry and physiology of the symbiosis. In natural and agricultural field settings, however, plants often interact with other members of the same species, which comprise a population. Plant–plant interactions within populations strongly influence basic processes such as growth and reproduction. Plant populations, as crops, are of fundamental importance to the welfare of the human population. Finally, the population is the fundamental unit of genetic adaptation to environmental heterogeneity (Raven, 1979 and references therein). For these reasons, studies of the effects of mycorrhizal fungi on plant populations are of considerable interest to the ecologist, evolutionary biologist and agronomist. We review here some of the important research illustrating four important ways in which mycorrhizal fungi influence plant populations. We include discussions on the positive effect of vesicular-arbuscular mycorrhizal colonization on plant reproduction and offspring survival, the relationship between plant population density and response to vesicular-arbuscular mycorrhizal colonization, the effect of vesicular-arbuscular mycorrhizal colonization on size and reproductive hierarchies within plant populations, and the role of established vesicular-arbuscular and ectomycorrhizal plants as important sources of inoculum for conspecific seedlings.

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* FAX No: 814-863-6139. E-mail: rxk13@psu.edu

Effects of mycorrhizal colonization on plant reproduction and offspring survival

Relatively little is known about the effects of mycorrhizal colonization on plant reproduction and, for technical reasons, this is especially true for perennial plant species. It is very difficult in most circumstances to maintain plants in a nonmycorrhizal condition for long, particularly in the field. Even when starting from sterile soil, chance inoculation by windblown or animal-dispersed inocula will eventually produce mycorrhizas. The necessity of life-long comparisons between mycorrhizal and nonmycorrhizal plants, however, is easily appreciated; the magnitude of mycorrhizal effects on reproduction early in the reproductive period may differ from that later in the period, even for annual species (Bryla and Koide, 1990a; Shumway and Koide, 1994b). Moreover, the effects of mycorrhizal fungi on reproduction of perennials may vary among years as nutrient availability varies among years. Extrapolation of lifetime reproduction from a single year, therefore, may not be particularly meaningful. Most hosts of ectomycorrhizal fungi are perennials and so we know essentially nothing about the effects of ectomycorrhizal fungi on the reproduction of their hosts.

Our knowledge of the effects of mycorrhizal fungi on plant reproduction is based almost entirely on annual, vesicular-arbuscular mycorrhizal plant species. For such species, a robust body of literature collectively shows that mycorrhizal colonization can significantly increase seed production (summarized in Koide, 2000). This is not surprising. Nitrogen and phosphorus frequently limit both vegetative growth and reproduction in terrestrial plants, and vesicular-arbuscular mycorrhizal fungi can improve host phosphorus status. Because ectomycorrhizal fungi can improve both nitrogen and phosphorus status of their hosts (Smith and Read, 1997), it is logical to suppose that colonization by ectomycorrhizal fungi would also increase plant reproduction, but this has not been demonstrated. Non-nutritional benefits from mycorrhizal colonization, such as a reduction in fungal pathogenesis, may also positively influence reproduction (Carey et al., 1992).

What is surprising, however, is that while vegetative size and reproductive output are often correlated (Bryla and Koide, 1990a and references therein), they may be influenced to very different extents by mycorrhizal colonization. In one experiment, *Abutilon theophrasti* plants were grown at a low density (12 m^{-2})in the field. Mycorrhizal colonization significantly increased vegetative growth when fertilizer phosphorus was not added to the soil, but failed to when fertilizer phosphorus was added. However, seed output was significantly increased by mycorrhizal colonization in both phosphorus treatments (Stanley et al., 1993). For two cultivars of *Lycopersicon esculentum*, reproductive trait responses to mycorrhizal colonization were greater than leaf area response (Poulton, 2000; Poulton et al., 2002). Other researchers have obtained similar results (Bryla and Koide, 1990b; Dodd et al., 1983; Koide et al., 1988). In many cases, the ability of vesicular-arbuscular mycorrhizal colonization to affect plants may be related to the plant phosphorus deficit, the difference between the demand for phosphorus by the plant and the phosphorus actually absorbed from the soil (Koide, 1991b). Thus, when there is a greater phosphorus deficit during reproduction than during vegetative growth, reproduction may be more responsive to mycorrhizal colonization (Fitter, 1989, 1991).

In a field study, Stanley et al. (1993) showed that as a consequence of significantly greater seed production in vesicular-arbuscular mycorrhizal swards of *Abutilon theophrasti*, seedling recruitment the following year was significantly greater in mycorrhizal plots than in nonmycorrhizal plots. The density of *Abutilon theophrasti* in mycorrhizal plots was about 175 plants m^{-2}, while the density in nonmycorrhizal plots was about 75 plants m^{-2}. Thus, early in succession, mycorrhizal colonization may immediately lead to greater densities. This may be particularly important for some early successional annual species for which rapid exploitation of space by the population is an important strategy.

Sexual reproduction consists of both male and female functions, and these may be influenced by mycorrhizal colonization independently. For example, in one cultivar of *Lycopersicon esculentum*, total pollen production per plant was significantly more responsive to mycorrhizal colonization than total seed production per plant (Poulton, 2000; Poulton et al., 2002). Thus, we discuss the male and female functions separately.

Female function

While the diploid embryo within a seed is genetically the product of both male and female gametophytes, we consider seed production to be primarily a female function. Provisioning of the endosperm and embryo with nutrients occurs within the ovary and, in angiosperms, the female contributes two-thirds of the genes to the triploid endosperm, the male one-third. Seed production can be significantly improved by mycorrhizal colonization. Presumably the major reason for this is the greater amount of resources possessed by mycorrhizal plants compared to nonmycorrhizal plants, but the proportional allocations of phosphorus or other resources to reproduction and vegetative growth may be altered by mycorrhizal colonization (Bryla and Koide, 1990b; Koide et al., 1988). Thus, the efficiency with which absorbed phosphorus is utilized to produce seeds may be different in mycorrhizal and nonmycorrhizal plants (Bryla and Koide, 1990a). Several components of seed production may be influenced by mycorrhizal colonization. For example, seed production by *Abutilon theophrasti* was increased by mycorrhizal colonization because mycorrhizal plants branched more extensively and consequently produced more flowers (Koide et al., 1994). Mycorrhizal colonization of *Abutilon theophrasti* also caused plants to flower for a longer period of time, and reduced the levels of fruit and seed abortion (Lu and Koide, 1994).

Male function

During pollen development, sporophyte tissues within the anther endow pollen grains with various storage products to be used during pollen tube growth. For example, phytate stored in the pollen grain is hydrolysed into phosphate and myo-inositol, which are used by the pollen tube for cell wall and membrane synthesis (Jackson and Linskens, 1982). The quantity and quality of pollen nutrient storage products can affect pollen germinability, tube growth rate, and the probability of siring seeds in competition with other pollen (Stephenson et al., 1994). It seems reasonable to expect mycorrhizal colonization to influence pollen quality in much the same way that it influences seed quality (see references in Koide, 2000). Indeed, we have shown recently for tomato (*Lycopersicon esculentum*) that mycorrhizal colonization can significantly increase *in vitro* pollen tube growth rate, which can allow pollen produced by mycorrhizal plants to outcompete slower growing pollen from nonmycorrhizal plants (Poulton et al., 2001a). This alone may result in mycorrhizal plants siring more seed than nonmycorrhizal plants (Poulton et al., 2001a). Moreover, mycorrhizal plants may produce more flowers (Poulton et al., 2001a), each of which may produce more pollen (Poulton et al., 2001b). Thus mycorrhizal colonization can improve male function in at least three ways.

Offspring vigor

Mycorrhizal colonization may result in enhanced offspring vigor and thus enhanced offspring survival. We first documented an effect of mycorrhizal colonization on seed quality in wild oat, *Avena fatua*. In this species, mycorrhizal colonization of the parent generation caused the offspring to grow faster (Koide and Lu, 1992; Lu and Koide, 1991). We therefore investigated the nutrient economy of the seeds and resultant seedlings. Mycorrhizal colonization of *Avena fatua* did not increase individual seed weight or seed nitrogen content, but increased seed phosphorus content by approximately 62% (Koide et al., 1988; Lu and Koide, 1991). Upon germination into a nonmycorrhizal soil, seeds produced by mycorrhizal plants were able to mobilize more phosphorus from the endosperm (about 50% of which was phytate) than seeds from nonmycorrhizal plants. Seedlings from mycorrhizal plants consequently contained significantly more phosphorus than seedlings from nonmycorrhizal plants.

Mycorrhizal colonization of *Abutilon theophrasti* increased weight, height, leaf area, lateral root formation and specific root length of offspring (Koide and Lu, 1995; Lewis and Koide, 1990) and the proportion of offspring plants that flowered (Shumway and Koide, 1994a). Seeds produced early in the reproductive phase were found to benefit more from mycorrhizal colonization than seeds produced later in the season (Shumway and Koide, 1994b), which is consistent with the observation that the number of arbuscules within a root system and thus the benefit from mycorrhizal colonization may be greatest in the earliest phases of growth (Smith and Dickson, 1991). By growing offspring plants in water, we showed that the superior growth of offspring produced by mycorrhizal parents was not due to a superior ability to take up nutrients (Koide and Lu, 1995). Instead, there was an inherent difference in initial growth rate (Koide and Lu, 1995). It is possible that the amount of phytate, the storage form of phosphorus in seeds, may have been more important than total phosphorus content in determining offspring vigor (Lewis and Koide, 1990).

A small but significant mycorrhizal effect on offspring vigor may not be particularly important when microsite variation is large or when germination is asynchronous. However, the effect may become very important when intraspecific competition among

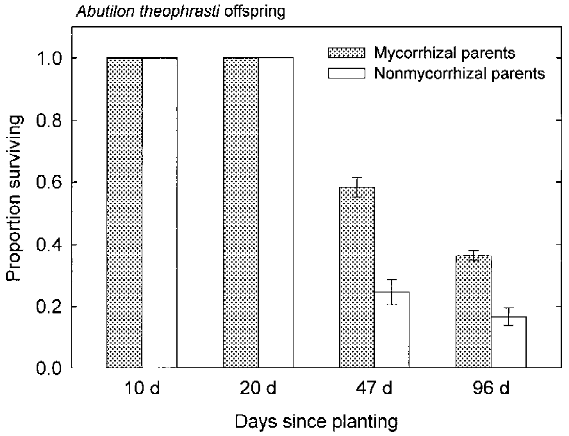

Figure 1. The mean (± S.E.M.) proportion of offspring from mycorrhizal and nonmycorrhizal *Abutilon theophrasti* parents surviving in dense, mixed populations of initially equal proportions. *n* = 8. See Heppell et al. (1998) for details. The differences are significant at 47 and 96 d after planting.

even-aged offspring is intense, as competition may greatly magnify small differences in size (Weiner and Thomas, 1986). Indeed, Solbrig (1981) indicates that during competition offspring size and fitness may be positively correlated. We therefore studied the consequences of mycorrhizal colonization of the parent generation of *Abutilon theophrasti* to the success of offspring under competitive conditions (Heppell et al., 1998). Seeds produced by mycorrhizal plants had 37% greater phosphorus concentrations, 6% greater weights, but did not differ significantly in nitrogen concentration. Seeds from mycorrhizal and nonmycorrhizal *Abutilon theophrasti* parents were germinated, and seedlings were planted in alternate 1.5 × 1.5 cm cells in large wooden boxes filled with a soil lacking mycorrhizal fungus propagules. The interior dimensions of the boxes were 50 cm × 50 cm × 32 cm high. All boxes were watered daily, but plants were not given fertilizer. Emergence did not differ significantly between offspring from mycorrhizal and nonmycorrhizal parents. However, after 20 d there were fewer offspring of nonmycorrhizal parents represented in the largest size classes and more offspring of nonmycorrhizal parents represented in the smallest size classes. As a result of self-thinning (mortality), only 42% of seedlings survived to 47 days. Mortality was not random with respect to parental treatment, however, as significantly more offspring from mycorrhizal parents survived compared to offspring from nonmycorrhizal parents (Figure 1). Offspring of mycorrhizal parents accounted for nearly all individuals in the larger size classes as well as the majority in the smallest size class, suggesting that many of the smallest offspring of nonmycorrhizal parents died. Thus, mycorrhizal colonization may influence more than one generation of plants.

Density-dependent responses to mycorrhizal colonization

The density of natural populations of plants varies widely for many reasons including varying levels of seed production and seedling mortality due to variation in resource availability. In any case, there is now substantial evidence that as density increases, the degree to which plants respond to vesicular-arbuscular mycorrhizal colonization decreases (Allsopp and Stock, 1992; Bååth and Hayman, 1984; Carey et al., 1992; Facelli et al., 1999; Hartnett et al., 1993; Hayman, 1983,; Koide, 1991a).

Three mechanisms have been proposed to account for this density-dependent effect of mycorrhizal colonization. The most likely explanation for this phenomenon is that at higher plant densities an increasing overlap of phosphorus depletion zones created by roots and root hairs results in a decreasing usefulness of hyphae for the acquisition of phosphorus (Figure 2; Hayman, 1983; Bååth and Facelli et al., 1999; Hartnett et al., 1993; Hayman, 1984; Koide, 1991a). If this is true, the effect of plant density on response to mycorrhizal colonization may differ among plant species. For example, species with a very sparse root system such as leek or onion may never have root densities high enough to render mycorrhizal hyphae superfluous, while species with dense root systems such as perennial ryegrass may, even at low plant densities, so effectively exploit soil that mycorrhizal fungi are nearly always superfluous (Koide, 1991b). In principle, a similar relationship between density and mycorrhiza responsiveness could occur for ectomycorrhizal hosts, but this has not yet been demonstrated.

A second possible reason for reduced plant response to mycorrhizal colonization at higher densities may be a reduction in mycorrhizal colonization (Allsopp and Stock, 1992; Bååth and Hayman, 1984; Koide, 1991a). Both the rate at which roots become colonized and the extent of colonization may have important consequences for the plant. For example, extensive colonization and increased phosphorus concentration of a seedling may increase its chances for

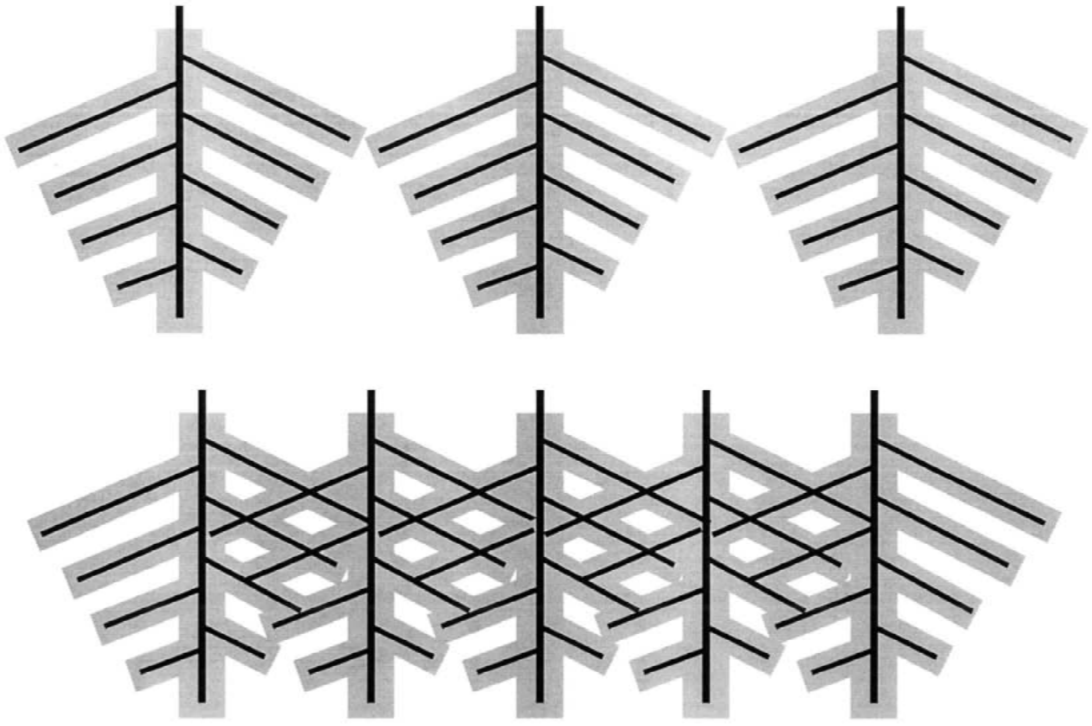

Figure 2. Thick black lines represent roots. Shading represents the phosphate depletion zone in the soil created by absorption of phosphate by roots and root hairs. Upper: Three widely spaced root systems do not very effectively exploit the soil volume. Thus, mycorrhizal hyphae can be effective in acquiring substantial phosphorus from unexploited soil. Lower: Five root systems occupy the same soil volume as the three above. In this case, roots and root hairs exploit much of the soil volume and mycorrhizal hyphae are largely superfluous.

survival and, remarkably, its reproductive effort (Barry and Miller, 1989). A given quantity of mycorrhiza inoculum in the soil can only colonize a given length of root in a given period of time. Thus, as root density increases, a smaller and smaller proportion of the total root length may become colonized in a given period of time. This may explain the results from experiments on *Abutilon theophrasti* (Koide, 1991a), *Aspalathus linearis* (Allsopp and Stock, 1992) and *Trifolium subterraneum* (Facelli et al., 1999) in which reduced proportions of the root systems were colonized at increased plant densities. It may also be possible that at higher densities, greater competition for light results in less carbohydrate available for mycorrhizal fungi (Abbott and Robson, 1984). Facelli et al. (1999) found, however, that reduced light levels do not necessarily result in less colonization.

In some cases, increasing plant density has been associated with *increasing* mycorrhizal colonization such as with the legume *Otholobium hirtum* (Allsopp and Stock, 1992) and with *Plantago lanceolata* (Eissenstat and Newman, 1990). The mechanism for this has not been shown, but the phenomenon is consistent with known positive effects of some root exudates and volatiles on hypha growth, hypha tropism and colonization of roots as shown by St. John et al. (1983), Gemma and Koske (1988) and Bécard and Piché (1989).

A third explanation involves the increase of the cost: benefit ratio of mycorrhizal colonization with increasing plant density (Allsopp and Stock, 1992). As plant density increases, competition for light increases and photosynthesis per plant declines. Plants may become limited more by carbon than by P. Thus, as the value of carbon to the plant increases and the value of phosphorus decreases, the beneficial effects of mycorrhizal colonization decrease. The effect of density on the cost:benefit ratio may differ among plant species. For example, grasses with upright leaves may suffer less from competition for light when densely packed than forbs with largely horizontal leaves (Begon et al., 1986). Therefore, grasses may suffer less proportional decline in responsiveness to mycorrhizal colonization than forbs as density increases.

In an experiment with onion described by Bååth and Hayman (1984), mycorrhizal fungi colonized a lower proportion of the root system at higher plant densities, despite using an amount of inoculum at each density that was proportional to the number of plants. This suggests that a simple 'dilution' of colonization at higher root densities is not the only cause of reduced colonization. Koide and Li (1991) showed that leachate from pots containing live roots of *Abutilon theophrasti* markedly reduced mycorrhizal colonization in other *Abutilon theophrasti* plants. This kind of density-dependent regulation of colonization may be important in maintaining a cost:benefit ratio that is favorable to the host. As root density increases and, therefore, as roots and root hairs more effectively explore the soil volume, mycorrhizal hyphae would become less and less useful (Bååth and Hayman, 1984; Koide, 1991a), increasing the cost:benefit ratio of maintaining them (Allsopp and Stock, 1992). Inherent mechanisms such as suggested by Koide and Li (1991) may maintain a lower cost:benefit ratio of the symbiosis to the plant.

The consequences of density-dependent responses to mycorrhizal colonization are potentially large. The lack of response of plants to mycorrhizal colonization in a number of field trials (McGonigle, 1988) may have many causes, but it may be that at high densities, common to many field crops, mycorrhizal colonization is not effective for one of the reasons discussed above (also see Facelli et al., 1999). Because at high densities crop growth may be largely unresponsive to mycorrhizal colonization, growers might improve economic efficiency by planting dense crops in soils of low inoculum density, but less dense crops in soils of high inoculum density. For wild species such as *Abutilon theophrasti*, colonization of one generation of plants at a comparatively low population density may lead to greater reproduction and thus a higher population density in the subsequent year (Stanley et al., 1993). Thus, members of the second year cohort would not benefit from colonization as much as the previous generation (Koide et al., 1994). Mycorrhizal fungi may thus serve to stabilize the density of natural plant populations through time.

The development of size and reproductive hierarchies within populations

The individuals comprising plant populations naturally vary in size. Some of this is due to microsite variation, some due to genetic variation. Grime et al. (1987) suggested that movement of assimilate from larger plants of one species to smaller plants of another species via vesicular-arbuscular mycorrhizal hyphae could account for greater community evenness (but see Robinson and Fitter, 1999). Such transport could have significant consequences for plant populations, resulting in a reduction in size disparity among individuals.

Most evidence, however, suggests that a reduction in size disparity within populations does not occur as a consequence of mycorrhizal colonization. Eissenstat and Newman (1990) indicated that the balance of competition between large and small *Plantago lanceolata* plants was not significantly influenced by mycorrhizal colonization. In other cases, mycorrhizal colonization resulted in a magnification rather than a diminution of inter-plant differences in size. For example, mycorrhizal colonization shifted the balance of competition in favor of larger *Prunella vulgaris* plants, not the smaller ones (Moora and Zobel, 1996), and mycorrhizal colonization resulted in an increase in the coefficient of variability (for size) in *Otholobium hirtum*, a species that is highly responsive to mycorrhizal colonization (Allsopp and Stock, 1992). Facelli et al. (1999) showed clearly that mycorrhizal colonization increased the intensity of intraspecific competition in *Trifolium subterraneum*, which resulted in greater size inequality. Carey et al. (1992) showed that among untreated (heavily mycorrhizal) *Vulpia ciliata* plants there were significantly more highly reproductive individuals than among the fungicide-treated (less mycorrhizal) plants, again suggesting that mycorrhizal colonization accentuates differences among individuals rather than reducing them. Shumway and Koide (1995) created mycorrhizal and nonmycorrhizal field populations of *Abutilon theophrasti* by soil fumigation and reinoculation, and obtained the same result as Carey et al. (1992); mycorrhizal populations had significantly higher inequality in terms of reproduction than nonmycorrhizal populations because the mycorrhizal populations had a higher frequency of highly reproductive individuals than nonmycorrhizal populations. Thus, it appears that slightly more robust plants are better able to capitalize on mycorrhizal colonization (Figure 3), possibly because phosphorus is transferred more freely to plants from which carbon is more available. We conclude, as did Facelli et al. (1999), that resource transfer via a common mycelial network does not appear to equalize resource distribution among intraspecific neighbours, and that movement of resources from larger to smaller plants via the mycorrhizal mycelium is not likely to have

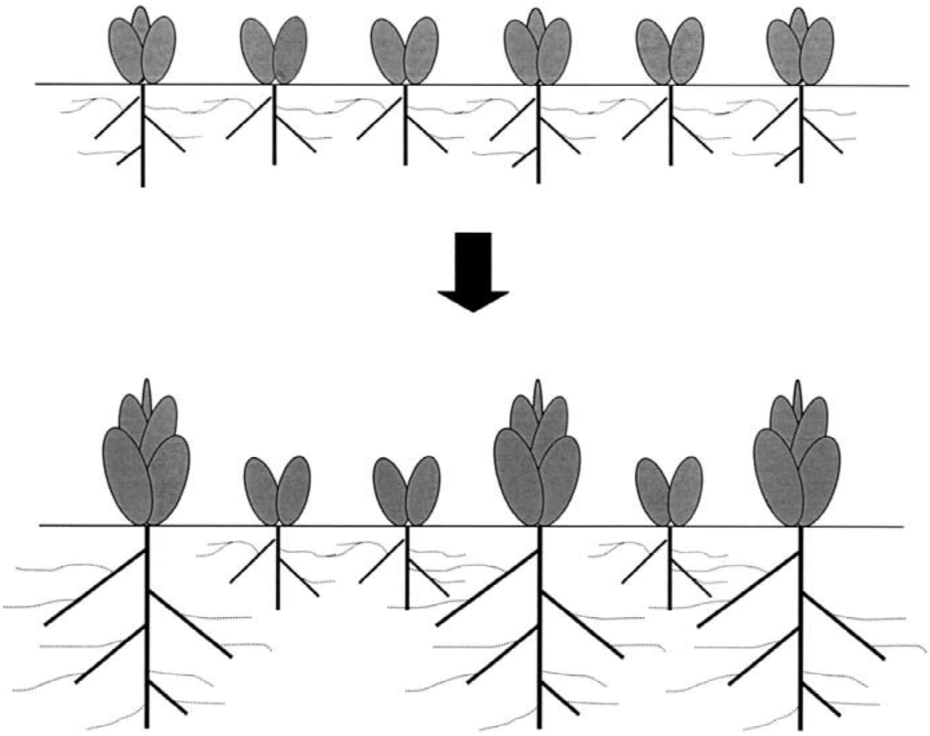

Figure 3. Thick black lines represent roots. Thin, dotted lines represent mycorrhizal hyphae. In most experiments to date, small, inherent differences among plants (note that the first, fourth and sixth plants are slightly larger than the others) are magnified by mycorrhizal colonization. This is contrary to the hypothesis that greater uniformity among plants should occur as a consequence of net resource transfer from dominant to suppressed individuals via a common mycelial network. Instead, the magnification of differences may result from greater phosphorus transfer to plants from which more carbon is available.

major ecological consequences. Instead, mycorrhizal fungi may result in an increased skewing of genetic representation in the next generation in favor of the dominant plants. If dominance has a genetic basis, the result could be a significant effect on population genetic structure (Facelli et al., 1999).

Mycorrhizal interactions between established plants and seedlings

Mycorrhizal networks and nutrient transfer

When seedlings establish within an existing mycorrhizal network, mycorrhizal linkages between established plants and seedlings may be formed (Newman, 1988). Autoradiographic evidence suggests that ^{32}P taken up by a fungal mycelium in microcosms is transferred both throughout the mycelium and into multiple host plants (Finlay and Read, 1986). A pre-existing mycelium may thus allow compatible seedlings to take advantage of a more extensive mycelial network than they otherwise could, and established plants may subsidize the costs of supporting this network (Newman, 1988).

Interest in mycorrhizal links has been raised by the possibility of net C transfer between plants. This may be particularly important to understory seedlings connected to mature canopy trees. Robinson and Fitter (1999) recently reviewed the literature on this subject and concluded that there is no evidence for significant net interplant C transfer through ectomycorrhizal or vesicular-arbuscular mycorrhizal links. Indeed, Fleming (1984) found that severing linkages between trees and seedlings actually increased seedling growth, and Simard et al. (1997) found that severing linkages caused no change in seedling height or dry mass. Again, it appears that if there is movement of resources between plants via mycorrhizal hyphae, it is not likely to have large consequences.

Seedling colonization

In many plant populations, seedlings grow near established plants and may thus become colonized by a preexisting mycorrhizal mycelium (Newman, 1988). This does not require that the established plants be living at the time of seedling growth, as shown by the positive influence of vesicular-arbuscular mycorrhizal winter cover crops on the mycorrhizal colonization of subsequent maize crops (e.g., Boswell et al., 1998; Kabir and Koide, 2000). Where vesicular-arbuscular mycorrhizal plants are absent, as in primary succession, lack of vesicular-arbuscular inoculum may limit succession (Allen, 1987). Low levels of mycorrhizal colonization also may reduce yields of agronomic crops (Boswell et al., 1998; Kabir and Koide, 2000). Thus, the provision of inoculum by previously established plants may be very important to newly establishing seedlings.

Because many ectomycorrhizal fungi produce abundant wind-dispersed spores, seedlings of ectomycorrhizal species may become rapidly colonized even in the absence of established plants (Allen, 1987). This is illustrated by ‘contaminant’ mycorrhizal colonization of seedlings grown in pasteurised soil in greenhouse studies (e.g., Pilz and Perry, 1984), the rapid ectomycorrhizal colonization of fumigated nursery beds by *Thelephora terrestris* (Marx and Cordell, 1987), and the establishment of ectomycorrhizal plants in primary succession (Allen, 1987; Trappe and Luoma, 1992). Nonetheless, in recent studies we found that *Quercus rubra* seedlings in a site surrounded by largely ectomycorrhizal forest were colonized to a much greater extent when planted near ectomycorrhizal trees than when planted near vesicular-arbuscular mycorrhizal trees (Dickie, 2000; Dickie et al., 2001). Lack of, or low extent of, colonization by ectomycorrhizal fungi may be an important factor preventing or reducing tree establishment following disturbance (Perry et al., 1989; Terwilliger and Pastor, 1999).

In addition to increasing the extent of seedling colonization, established plants may also influence the species of fungi that colonize seedlings (Last et al., 1992 and citations therein). Seedlings establishing in forest clearcuts may be colonized by different species of fungi than seedlings establishing at forest edges or within the forest (e.g., Kranabetter and Wylie, 1999). Even where seedlings establish within the root zone of established trees, the distance to the nearest tree may influence the composition of mycorrhizal fungal species (Gibson and Deacon, 1988). It appears that some species of fungi are largely incapable of colonizing seedlings except through hyphae extending from established tree roots, as trenching can substantially alter the community composition of fungi colonizing seedlings (Fleming, 1984; Simard et al., 1997).

Established plants may influence succession and regeneration if they control to a large extent either the degree of mycorrhizal colonization of seedlings or the species composition of the colonizing fungi. Succession may be hastened when at least some mycorrhizal fungal species colonizing the established individuals of one species are capable of colonizing the seedlings of the succeeding plant species, and it may be hindered when there is no such compatibility. Cross-species compatibility is obviously not necessary for regeneration of a given plant species, however, since this would only require that the fungi supported by the established individuals are capable of colonizing conspecific seedlings. An inability of the fungi to colonize both established plants and seedlings could negatively affect regeneration. Established plants could conceivably influence the distribution of other plants by providing the appropriate mycorrhizal fungi. One might, therefore, hypothesize that ectomycorrhizal tree species would be patchily distributed in primarily vesicular-arbuscular mycorrhizal forest, and vice versa.

Influences of established plants on the species composition of vesicular-arbuscular mycorrhizal fungi colonizing seedlings have been less well studied than in ectomycorrhiza. Vesicular-arbuscular mycorrhizal fungi are generally believed to be less diverse than ECM fungi, and to have lower levels of host specificity. Nonetheless, communities of vesicular-arbuscular mycorrhizal fungi in soils may differ depending on the presence of different host plant species (Johnson et al., 1992; McGonigle and Fitter, 1990), and this could result in different species of fungi infecting seedlings. The recent development of molecular approaches to identify vesicular-arbuscular mycorrhizal fungi in individual roots may permit further advances in this area.

Net influence of established plants on seedlings

We have found that *Quercus rubra* seedlings planted near established ectomycorrhizal trees had increased ectomycorrhizal colonization, nitrogen and phosphorus uptake, and growth compared with seedlings planted near vesicular-arbuscular mycorrhizal trees (Dickie, 2000; Dickie et al., in press). Nonetheless, although established plants may have beneficial influences on seedlings in terms of mycorrhizal colonization, the net influence of established plants on seedlings may be negative. For example, Zhou and Sharik (1997) found that *Quercus rubra* seedling growth was maximized in forest clearcuts, although mycorrhizal colonization was highest at intermediate canopy levels. Mycorrhizal colonization was reduced under a full canopy, perhaps due to reduced seedling photosynthesis (Zhou et al., 1997). Negative influences of established plants on seedlings may occur either directly, through competition, or indirectly through support of pathogenic organisms (Packer and Clay, 2000). It appears that the net influence of established plants on seedlings is most likely to be positive in sites where lack of mycorrhizal colonization would limit seedling growth; net negative interactions are more likely as plant density increases.

Conclusions

Populations possess properties that individuals do not. Thus, the effects of mycorrhizal fungi on populations of plants are not simply the sum of their effects on the individuals within a population. The study of mycorrhizas at this higher level of complexity is therefore of great importance to ecologists who seek to understand their role in natural ecosystems, and to agronomists who seek practical applications of them in agricultural systems. The research reviewed herein indicates that mycorrhizal fungi can interact with plant populations in several important ways. Reproduction and offspring survival can be significantly increased by vesicular-arbuscular mycorrhizal colonization, and this can increase plant population size, at least in the short term. The effects of mycorrhizal colonization on reproduction can be manifested through both the male and female functions. This effect on reproduction, however, may not occur generation after generation because of the density dependence of response to mycorrhizal colonization. Because low-density populations may benefit more from mycorrhizal colonization than high-density populations, mycorrhizal fungi may contribute to the stabilization of population density through time. There is no evidence that variation among individuals within populations is reduced by vesicular-arbuscular mycorrhizal colonization as predicted from the few studies suggesting that significant quantities of materials may be transferred from more vigorous to less vigorous individuals. Instead, differences among individuals may actually be exacerbated by mycorrhizal colonization. Finally, previously established plants may influence seedlings of the same species by providing an important source of mycorrhiza inoculum - living hyphae. In agricultural systems, winter cover crops that support vesicular-arbuscular mycorrhizal fungi thus benefit subsequent mycorrhizal crops. In natural ecosystems in which inoculum is limited, this pattern of colonization may naturally result in patchy distributions of vesicular-arbuscular, ecto- or ericoid mycorrhizal plants. These interactions between mycorrhizal fungi and plant populations suggest that further research on the effects of mycorrhizal fungi at the level of the plant population will continue to be valuable in both ecological and agricultural contexts.

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