IDEAS AND PERSPECTIVES

The mycorrhizal dependence of subordinates determines the effect of arbuscular mycorrhizal fungi on plant diversity

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Abstract

It is widely recognized that arbuscular mycorrhizal fungi (AMF) influence plant community structure. Several studies in the past few years have focused on the effect of AMF on plant diversity, showing contradictory results. On the basis of studies carried out in grasslands, it has been proposed that these results may not be in conflict but rather depend on mycorrhizal dependence of dominant and subordinate species in the plant community. Here, we propose a simple conceptual model to explain the effect of AMF on plant diversity and dominance hierarchy. Our model suggests that the effect of AMF on plant diversity can be explained mainly by mycorrhizal dependence of subordinates. It also gives predictions for a wider range of community types, and helps in identifying the systems in which empirical data are most critically needed.

Keywords

Arbuscular mycorrhizas, dominance hierarchies, mycorrhizal dependence, plant diversity.

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INTRODUCTION

In exchange for the carbohydrates they receive from them, arbuscular mycorrhizal fungi (AMF) benefit plants in many ways, such as improved nutrient acquisition, protection of roots against pathogens, alleviation of water stress and enhanced competitive ability (Smith & Read 1997). The degree of mycorrhizal dependence and the cost–benefit relationship vary among species and according to the genotype of the fungi involved in the relationship and the abiotic and biotic context (e.g. soil nutrients, interactions with other organisms). Mycorrhizal-dependent plant species are likely to obtain more benefit from AMF than species with a lower mycorrhizal dependence (van der Heijden 2002). Because of this, mycorrhizal fungi can have a large influence on the structure and functioning of natural communities and ecosystems (Hartnett & Wilson 2002). They may affect the competitive abilities of mycorrhizal plant species through differential benefits to the host plants (Hetrick *et al.* 1989; Marler *et al.* 1999; Callaway *et al.* 2001). They may also mediate plant competition by the inter- and intraspecific transfer of assimilates through a common mycorrhizal network (Francis & Read 1984; Grime *et al.* 1987), although the ecological relevance of this mechanism is still controversial (Simard *et al.* 2002).

In the past few years, and with the growing research interest in the links between biodiversity and ecosystem functioning (Loreau *et al.* 2001), some studies have been carried out or revisited in order to elucidate the way in which AMF influence plant community structure (Grime *et al.* 1987; Gange *et al.* 1993; Newsham *et al.* 1995; van der Heijden *et al.* 1998; Hartnett & Wilson 1999). It is widely accepted that mycorrhizal fungi affect plant diversity (Read 1998; Leake 2001); nevertheless, the few experiments that have directly explored these relationships have shown contradictory results (reviewed by Hartnett & Wilson 2002). Some of them have shown a positive relationship between the presence of AMF and plant diversity (Grime *et al.* 1987; Gange *et al.* 1993; van der Heijden *et al.* 1998), while others have reported the opposite (Newsham *et al.* 1995; Hartnett & Wilson 1999). These results may not necessarily be in conflict and the outcome may be highly dependent on plant mycorrhizal dependence and position in the local dominance hierarchy (Hartnett & Wilson 2002; van der Heijden 2002). We propose a model that predicts that the presence of AMF will decrease the steepness of the plant dominance–rank curve, and thus beget plant diversity, only in systems where most of the subordinate plant species are mycorrhizal. In other systems, AMF are predicted to have nil or negative effect on plant diversity. Our model integrates previous conceptual ideas (Bergelson & Crawley 1988; Hartnett & Wilson 1999, 2002; van der Heijden 2002) and empirical results (see below), mainly from grasslands, into a formalized, consistent context that allows predictions for a wider range of ecosystem types.

THE CONCEPTUAL MODEL

We propose a simple conceptual model of the effects of AMF on diversity of plant communities, based on different degrees of mycorrhizal dependence of plants with different positions in the dominance hierarchy (Fig. 1). It is known that plant dependence varies with different fungal genotypes involved in the relationship (van der Heijden *et al.* 1998). However, for the sake of simplicity, this model assumes that the plant dependence is a function of the fungal assemblage that occurs in the community in which the model is to be used, and therefore may vary if other fungal genotypes are to be involved in the relationship. When most plant species in a community are non- or low-mycorrhizal dependent, AMF are not expected to exert an effect on plant community composition, at least in the short term (situation 1 in Fig. 1). If the dominants are highly mycorrhizal, and the subordinates are not, then AMF should increase the steepness of the dominance–rank curve and thus decrease plant diversity, with the main mechanism being an enhanced competitive ability of the dominants (situation 2 in Fig. 1). If the subordinates are strongly mycorrhizal and the dominants are not, then AMF may ameliorate the steepness of the dominance–rank curve and thus increase diversity (situation 3 in Fig. 1). If both the dominants and subordinates are mycorrhizal, then AMF should ameliorate the steepness of the dominance–rank curve and increase plant diversity. One possible mechanism for this could be redistribution of assimilates from dominants to subordinates through a common mycorrhizal network, but, as stated above, this mechanism is still controversial and more conclusive evidence is needed on its ecological relevance in the field (situation 4 in Fig. 1). It should be noted that in our model, in situations in which mycorrizas are a normal component of the system, the knowledge of the mycorrhizal dependence of subordinates is more informative than that of the dominants. If subordinate species are highly mycorrhizal dependent, plant diversity should increase in the presence of mycorrhizal fungi, irrespective of the mycorrizal dependence of dominants (situations 3 and 4 in Fig. 1). In contrast, if the degree of mycorrhizal dependence of the dominants, but not that of the subordinates, is known, it is not possible to predict whether plant diversity should increase (situation 4 in Fig. 1) or decrease (situation 2 in Fig. 1) in the presence of mycorrhizal fungi.

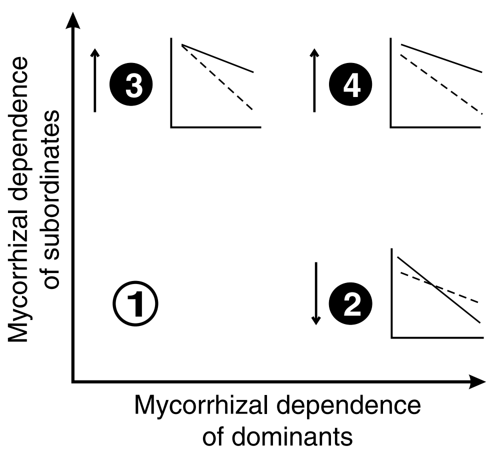

Figure 1 Conceptual model representing the effects of the presence arbuscular mycorrhizal fungi (AMF) on plant community diversity. Solid circles represent situations where AMF exert a significant effect on plant diversity. The empty circle represents situations where AMF do not exert a significant effect on plant community diversity (at least in the short term) because both dominant and subordinates are non-mycotrophic or weakly mycotrophic. The arrows represent the direction of the effect of AMF on plant diversity (increase/decrease). The small figures on the right of each circle represent the effect of AMF on the dominance–rank curve: solid lines, AMF present; dashed lines, AMF absent.

EMPIRICAL DATA

Typical examples of situation 1 in Fig. 1 are early-successional (Reeves *et al.* 1979; Allen *et al.* 1992) or salt-marsh communities (Juniper & Abbott 1993). However, although AMF do not seem to have any immediate effect on the structure of early-successional communities, they may accelerate or facilitate successional changes allowing mycotrophic species to establish (Gange *et al.* 1990).

An example of situation 2 in Fig. 1 is the lichen-rich heath community studied by Newsham *et al.* (1995). There, the suppression of lichen-forming and AM fungi by fungicide application increased species richness by improving the growth of non- or low-dependent mycorrhizal vascular plants and mosses. Another example is the tall-grass prairie experiment reported by Hartnett & Wilson (1999). In this case, the suppression of AMF resulted in a decrease in abundance of the dominant, obligatory mycotrophic C_4 tall grasses (*Andropogon gerardii*, *Sorghastum nutans* and *A. scoparius*), a compensatory increase in abundance of many facultatively mycotrophic subordinate C_3 grasses and forbs, and a consequent increase in plant diversity. In a semiarid Australian herbland, plant species diversity increased when mycorrhizal colonization was suppressed because growth of the highly mycorrhizal-responsive dominant *Medicago minima* was reduced and subordinate plant species were released from competition (O'Connor *et al.* 2002). Together with the decrease of the dominant, the aboveground biomass of the two main subordinates (non-mycotrophic *Carrichtera annua* and mycotrophic but non-mycorrhizal dependent *Salvia verbenaca*) significantly increased, enhancing plant species richness and evenness and thus altering the steepness of the dominance–rank curve as proposed for situation 2 in Fig. 1.

Examples of communities corresponding to situation 3 in Fig. 1 are coastal fynbos dominated by non-mycorrhizal Proteaceae and Restionaceae (Allsopp & Stock 1993) and communities dominated by non-mycorrhizal sedges (Cyperaceae) (Smith & Read 1997).

Many experimental studies on the effect of AMF on plant community diversity have been performed on systems where the majority of the plant species are mycorrhizal, which correspond to situation 4 in Fig. 1. Consistent with our model, they all tended to show positive effects of AMF on plant diversity. For example, in a microcosms experiment, Grime *et al.* (1987) showed that the addition of AMF increased plant diversity of calcareous grassland microcosms because of the transfer of assimilates from canopy dominants to understorey components through a common mycorrhizal network. van der Heijden *et al.* (1998) also showed that the presence of AMF increased plant diversity of calcareous grassland and old-field model communities, and proposed that different plant species benefited from different AMF taxa. Gange *et al.* (1993) found that the reduction of fungal infection by a fungicide resulted in lower plant species richness in calcareous grassland field plots. They argued that seedling recruitment was lower when AMF were suppressed.

DISCUSSION

The importance of studies focusing on the relationship of AMF, plant community structure and ecosystem functioning has been recently stressed (Read 1998; Leake 2001). The differential responsiveness of different plant species as a mechanism in which AMF influence plant community structure was first proposed by Bergelson & Crawley (1988) and later supported by the work of Hartnett & Wilson (1999) and O'Connor *et al.* (2002). Hartnett & Wilson (2002) and van der Heijden (2002) have suggested that the number and relative abundance of mycorrhizal-dependent plant species in the species pool can be used to predict how AMF affect communities. However, most studies to date have been carried out in grasslands. Here, we propose a simple, general model that predicts the diversity response of a broad range of natural plant communities to AMF (or their suppression) on the basis of (a) the mycorrhizal dependence of subordinates and to a lesser degree that of the dominants; and (b) the steepness of the dominance–rank curve. Both are relatively easy to assess, and for some regions of the world (e.g. Europe, USA) this information is already available. To our knowledge, all the empirical evidence published to date matches the prediction of our model. However, most reports correspond only to situations 2 and 4 in Fig. 1. What is needed now, in order to fully validate the predictions of the model, is the setting up of standard experiments in communities other than grasslands, and including all the extreme combinations illustrated in Fig. 1, especially those poorly covered so far, such as situations where non- or low-mycorrhizal species dominate.

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REFERENCES

Allen, M.F., Clouse, S.D., Weinbaum, B.S., Jeakins, S., Friese C.F. & Allen, E.B. (1992). Mycorrhizae and the integration of scales: from molecules to ecosystems. In: *Mycorrhizal Functioning* (ed. Allen, M.F.). Chapman & Hall, London, pp. 488–515.

Allsopp, N. & Stock, W.D. (1993). Mycorrhizal status of plants in the Cape floristic Region, South Africa. *Bothalia*, 23, 91–104.

Bergelson, J.M. & Crawley, M.J. (1988). Mycorrhizal infection and plant species diversity. *Nature*, 334, 202.

Callaway, R., Newingham, M.B., Zabinsky, C.A. & Mahall, B.E. (2001). Compensatory growth and competitive ability of an invasive weed are enhanced by soil fungi and native neighbours. *Ecol. Lett.*, 4, 429–433.

Francis, R. & Read, D.J. (1984). Direct transfer of carbon between plants connected by vesicular mycorrhizal mycelium. *Nature*, 307, 53–56.

Gange, A.C., Brown, V.K. & Farmer, L.M. (1990). A test of mycorrhizal benefit in early successional plant community. *New Phytol.*, 115, 85–91.

Gange, A.C., Brown, V.K. & Sinclair, S. (1993). Vesicular–arbuscular mycorrhizal fungi: a determinant of plant community structure in early succession. *Funct. Ecol.*, 7, 616–622.

Grime, J.P., Mackey, J.M., Miller, S.H. & Read, D.J. (1987). Floristic diversity in a model system using experimental microcosm. *Nature*, 328, 420–422.

Hartnett, D.C. & Wilson, G.W.T. (1999). Mycorrhizae influence plant community structure and diversity in tallgrass praire. *Ecology*, 80, 1187–1195.

Hartnett, D.C. & Wilson, G.W.T. (2002). The role of mycorrhizas in plant community structure and dynamics: lessons from grasslands. *Plant Soil*, 244, 319–331.

van der Heijden, M.G.A. (2002). Arbuscular mycorrhizal fungi as a determinant of plant diversity: in search of underlying mechanisms and general principles. In: *Mycorrhizal Ecology* (eds van der Heijden, M.G.A. & Sanders, I.). Ecological Studies, Vol. 157, Springer-Verlag, Berlin, pp. 243–265.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Stritwolf-Engel, R., Boller, T. *et al.* (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, 396, 69–72.

Hetrick, B.A.D., Wilson, G.W.T. & Hartnett, D.C. (1989). Relationships between mycorrhizal dependence and competitive ability of two tall grass prairie grasses. *Can. J. Bot.*, 67, 2608–2615.

Juniper, S. & Abbott, L. (1993). Vesicular–arbuscular mycorrhizas and soil salinity. *Mycorrhiza*, 4, 45–57.

Leake, J. (2001). Is diversity of ectomycorrhizal fungi important for ecosystem functioning? *New Phytol.,* 152, 1–8.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. *et al.* (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.

Marler, M.J., Zabinski, C.A. & Callaway, R.M. (1999). Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology*, 80, 1180–1186.

Newsham, K.K., Watkinson, A.R., West, H.M &. Fitter, A.H. (1995). Symbiotic fungi determine plant community structure: changes in a lichen-rich community induced by fungicide application. *Funct. Ecol.*, 9, 442–447.

O'Connor, P.J., Smith, S.E. & Smith, F.A. (2002). Arbuscular mycorrhizas influence plant diversity and community structure in a semiarid herbland. *New Phytol.*, 154, 209–218.

Read, D.J. (1998). The ties that bind. *Nature*, 396, 22–23.

Reeves, F.B., Wagner, D., Moorman, T. & Kiel, J. (1979). The role of endomycorrhizae in revegetation practices in the semi-arid west. I. Comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *Am. J. Bot.*, 66, 6–13.

Simard, S.W., Jones, M.D. & Durall, A. (2002). Carbon and nutrient fluxes within and between mycorrhizal plants. In: *Mycorrhizal Ecology* (eds van der Heijden, M.G.A. & Sanders, I.). Ecological Studies, Vol. 157, Springer-Verlag, Berlin, pp. 33–74.

Smith, S.E. & Read, D.J. (1997). *Mycorrhizal Symbiosis,* 2nd edn. Academic Press, New York.

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