

The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity

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Abstract

Ecological theory predicts a positive and asymptotic relationship between plant diversity and ecosystem productivity based on the ability of more diverse plant communities to use limiting resources more fully. This is supported by recent empirical evidence. Additionally, in natural ecosystems, plant productivity is often a function of the presence and composition of mycorrhizal associations. Yet, the effect of mycorrhizal fungi on the relationship between plant diversity and productivity has not been investigated. We predict that in the presence of AMF, productivity will saturate at lower levels of species richness because AMF increase the ability of plant species to utilize nutrient resources. In this study we manipulated old-field plant species richness in the presence and absence of two species of AMF. We found that in the absence of AMF, the relationship between plant species richness and productivity is positive and linear. However, in the presence of AMF, the relationship is positive but asymptotic, even though the maximum plant biomass was significantly different between the two AMF treatments. This is consistent with the hypothesis that AMF increase the redundancy of plant species in the productivity of plant communities, and indicates that these symbionts must be considered in future investigations of plant biodiversity and ecosystem function.

Keywords

Arbuscular mycorrhiza, biodiversity, ecosystem function, plant–microbe interactions.

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INTRODUCTION

Recently, researchers have been investigating the potential relationship between species diversity and ecosystem functioning (Naeem *et al.* 1994; Tilman & Downing 1994; Tilman *et al.* 1996; Naeem & Li 1997). Several different theories about the nature of this relationship have emerged (Johnson *et al.* 1996). Empirical tests of these theories have focused mainly on plant communities, whose ability to photosynthesize makes them crucial components of terrestrial ecosystems. Often, the ecosystem response measured has been the productivity of the plant community. But the relationship between diversity and plant productivity has not proven easy to determine. While some researchers agree that increasing plant diversity increases productivity (Naeem *et al.* 1994, 1995; Tilman *et al.* 1996, 1997), it is uncertain at what level of species richness this response reaches a maximum, as predicted by redundancy-type models. In addition, critics of these studies are concerned that factors like soil nutrient status or other “hidden treatments” may be

obscuring the true relationship between diversity and productivity (Givnish 1994; Huston 1997).

We would like to add that the relationship between plant diversity and productivity may be confounded by differences among functional groups that interact directly with primary producers. One such group of organisms is the arbuscular mycorrhizal fungi (AMF) found in the soil. These fungi form intimate associations with the roots of about 85% of all terrestrial plants, and can greatly increase a plant's uptake of soil nutrients, especially phosphorus (Smith & Read 1997). The plant, in return, provides photosynthate needed by the fungus. As a result of this relationship, AMF have the potential to greatly affect plant productivity (Janos 1980; van der Heijden *et al.* 1998a). Perhaps more importantly, AMF have been shown to have a strong influence on the outcome of competition between plants (Fitter 1977; Allen & Allen 1984; Hetrick *et al.* 1989; Bever *et al.* 1997), as well as plant community diversity (Gange *et al.* 1990; Chiariello *et al.* 1982; Grime *et al.* 1987; Newman & Reddell 1988; Streitwolf-Engel *et al.* 1997; van der Heijden *et al.* 1998a, b; Hartnett &

Wilson 1999). Curiously, AMF are not often considered in discussions of plant diversity experiments, despite this wealth of evidence implicating them in plant community dynamics. Furthermore, it is standard practice to sterilize the soil during the set-up of plant diversity experiments. This is done to remove the existing seed bank, which would make it easier to manipulate plant species richness using an exogenous seed source. However, this practice may also eliminate other interacting soil organisms, such as AMF, and their status during such experiments is often not very clear.

Tilman *et al.* (1997) present a “generalized niche model”, which predicts that community biomass will asymptotically increase with species diversity. Their model is based on interspecific differences in the use of resources by plants as a means for more diverse plant communities to use limiting resources more fully, and therefore to achieve greater productivity. We propose a model similar to that of Tilman *et al.* (1997) that incorporates AMF. We depict a habitat in which two soil resources limit plant species abundances, using two axes of resource space differentiation (Fig. 1). Each plant species would have some limited range within this two-dimensional resource space at which it could exploit these resources. This range is represented by circles (Fig. 1). In the presence of AMF, the range covered by each plant is expanded since the fungus can extend its external mycelium out farther than is possible by roots alone, providing access to more resources for the symbionts.

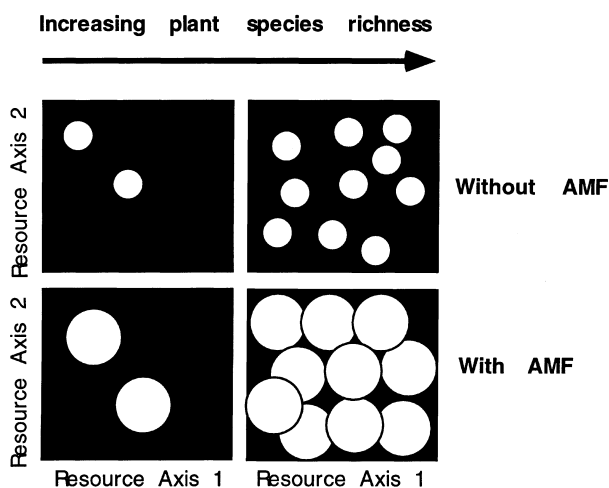


Figure 1 A conceptual model representing a habitat in which two soil resources (Axes 1 and 2) limit plant species abundance (modified from Tilman *et al.* 1997). Circles represent the range at which each plant species could exploit these resources. Arbuscular mycorrhizal fungi (AMF) increase this range. The model predicts that community biomass will asymptotically increase with species diversity, and that the asymptote will be reached with fewer plant species in the presence of AMF.

Also, the fungi also possess unique enzymes such as phosphatases and proteinases (Smith & Read 1997) that can increase nutrient availability. It is important to note that AM fungi will not likely extend a plant’s range of resource acquisition along all resource axes in a uniform manner, and that the pattern in nature is likely to be a complex function of local abundance of limiting resources. However, even without such a uniform expansion on all resource axes, the end result is that the resource space (boxes) is completely permeated and, thus, productivity should reach a maximum with fewer plant species. As a result, AMF should increase the redundancy of plant species on the productivity of plant communities.

In this paper, we manipulated plant species richness and AMF in macrocosms to test the following hypotheses: (i) there is a positive but asymptotic relationship between plant species richness and productivity, and (ii) in the presence of AMF, productivity will reach an asymptote at lower levels of species richness.

METHODS

The experiment was set up at the Long-Term Mycorrhiza Research Site (LTMR) located within the University of Guelph Nature Reserve, in Guelph, Canada (Klironomos 1999). The experimental units were arranged in a fully randomized manner using a 3×6 factorial design, where one factor was AMF species (*Glomus etunicatum* Becker & Gerdemann, *Glomus intraradices* Schenck & Smith, or nonmycorrhizal control), and the second factor was plant species richness (0, 1, 2, 5, 10, or 15 species). Each treatment combination was replicated five times, for a total of 90 experimental units. Each experimental unit consisted of a macrocosm (1 m \times 0.75 m \times 0.5 m deep) filled with 90 kg of a 1:1 mixture of gamma-irradiated field soil and silica sand. To each macrocosm, we added 1 kg sheared leek-roots that were infected by one of the AMF. This AMF inoculum was placed 5 cm below the surface of the soil. The macrocosms were then showered with 1500 seeds, comprising one of the six levels of species richness. Plant species were randomly selected from the following 35 plants that coexist at the LTMR: *Agrostis gigantea* Roth., *Bromus inermis* Leysser, *Festuca pratensis* Hudson., *Poa compressa* L., *Phleum pratense* L., *Dactylis glomerata* L., *Achillea millefolium* L., *Asclepias syriaca* L., *Aster lanceolatus* Willd., *Aster macrophyllus* L., *Aster cordifolius* L., *Aster novae-angliae* L., *Cerastium vulgatum* L., *Cirsium arvense* (L.) Scop., *Cicorium intybus* L., *Chrysanthemum leucanthemum* L., *Daucus carota* L., *Echium vulgare* L., *Erigeron annuus* (L.) Pers., *Euthamia graminifolia* (L.) Nutt., *Fragaria virginiana* Duchesne, *Geum macrophyllum* Willd., *Hypericum perforatum* L., *Linaria vulgaris* Miller., *Medicago lupulina* L., *Plantago*

lanceolata L., *Plantago major* L., *Potentilla recta* L., *Prunella vulgaris* L., *Ranunculus acris* L., *Rudbeckia hirta* L., *Solidago canadensis* L., *Solidago altissima* L., *Trifolium pratense* L., and *Oenothera biennis* L.

Plants were allowed to grow for 20 weeks, after which roots and shoots were harvested and total biomass was determined by drying at 80°C for 48 h. The study was performed in the summer of 1997 and replicated in the summer of 1998 (total of 180 experimental units). The data were analysed using a factorial analysis of variance (ANOVA), where the factors were (i) AMF and (ii) plant species richness, and the dependent variable was total plant biomass. The relationship between plant diversity and plant biomass, within each AMF treatment, was then analysed in more detail. We performed regressions using linear, power, log, exponential and polynomial functions, and assessed coefficients of determination for best fit. The data from 1997 and 1998 were originally analysed separately, but no significant year differences were found; thus all data were pooled for a single analysis.

RESULTS

We observed successful germination and growth of all plant species in each of the treatments. However, total plant biomass within the macrocosms was influenced by plant species richness ($F_{5,162} = 6.88$, $P = 0.0001$) and by AMF ($F_{2,162} = 8.21$, $P = 0.0001$). Increasing plant species richness generally increased total plant biomass at final harvest (averaged over all AMF treatments). On the other hand, association with AMF either stimulated (*G. etunicatum*) or reduced (*G. intraradices*) plant biomass compared with the non-AMF control (averaged over all plant richness treatments).

We also found a significant interaction between plant richness and AMF ($F_{15,162} = 5.87$, $P = 0.0001$). In fact, the presence and species of AMF significantly influenced the nature of the relationship between plant diversity and productivity (Fig. 2). In the absence of AMF, the relationship was positive and linear, and supported the diversity-productivity hypothesis. However, in the presence of either AMF, linearity was not the best fit; rather, plant biomass reached a plateau after only two plant species (power function was a best fit), and thus more likely supports the redundancy hypothesis.

At all plant richness levels, total plant biomass was significantly higher when associated with *G. etunicatum*. In fact, it was more than 100% higher than when associated with *G. intraradices*. At richness levels below 10 plant species, no significant difference in biomass was found between *G. intraradices* and the non-AMF control. However, at the highest plant richness treatment, *G. intraradices* suppressed plant biomass.

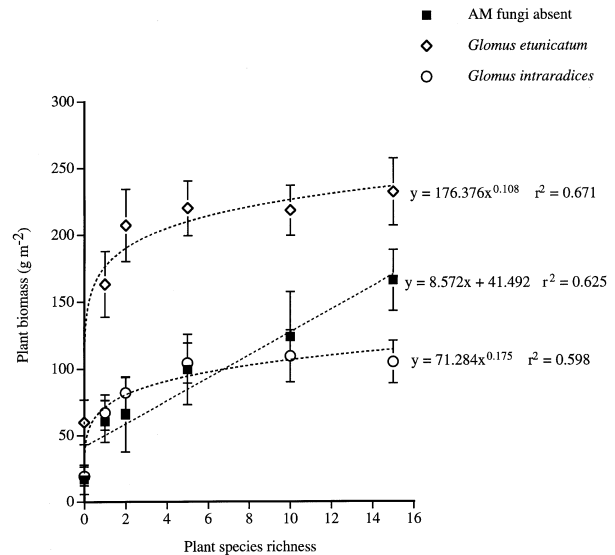


Figure 2 The relationship between plant species richness and biomass of an old-field plant community in the presence (*G. etunicatum* or *G. intraradices*) or absence of arbuscular mycorrhizal fungi. Error bars represent ± 1 SE. Lines represent the best fit with linear, power, log, exponential and polynomial functions.

DISCUSSION

These results support the hypothesis of a positive but asymptotic relationship between plant species richness and productivity, but only in the presence of AMF. In the absence of AMF the relationship was also positive, but we did not detect an asymptote in productivity within the 15-species range. It is unlikely that such a linear response would be sustained across a wider range of plant diversities, but it is not possible to predict the exact point at which the productivity curve would flatten. Regardless, this supports the prediction that mycorrhizal plant communities reach an asymptote at lower levels of plant species richness, and that AMF reduce the impact of plant species deletions on the productivity of plant communities.

Plant biomass reached a maximum at less than 10 plant species for both AMF treatments, even though the amplitude of the curves differed significantly. The difference in overall biomass between the two different AMF treatments can be explained by the fact that AMF can exist anywhere along the mutualism-parasitism continuum (Johnson *et al.* 1997). Fungi differ in their place along the continuum as described by carbon costs of mineral nutrient gains. The *G. intraradices* isolate used in this study has been shown to extract a higher carbon cost for plant nutrient gains than *G. etunicatum*. In both cases, the combination of plants and AMF results in a more efficient extraction of nutrients from soil. However, the

amount of resources available to plant communities is reduced in the presence of AMF, which exert a very high carbon demand compared with non-AMF systems. Thus, when associated with *G. intraradices* and *G. etunicatum* the two-dimensional resource space is permeated with fewer plant species, but in the former, production is not augmented. Rather it is suppressed.

In natural ecosystems, plant communities are associated with communities of AMF (Johnson *et al.* 1991; Helgason *et al.* 1998). These fungal communities are presumably comprised of genotypes that are mutualists as well as cheaters (parasites). Also, for many fungi, their position along the parasitism-mutualism continuum will depend on the plant symbiont (van der Heijden *et al.* 1998b; Klironomos 1999), as well as edaphic factors (Johnson 1993). Therefore based on the present results we can predict that the presence of AMF will result in a maximum productivity with fewer plant species. However, the exact value of this maximum productivity will depend on the exact carbon costs of the associated fungal communities. For example, ecosystems that have been heavily impacted by humans contain fewer AMF isolates (Helgason *et al.* 1998) and these are less efficient at providing mineral benefits to plants (Johnson 1993). The presence of such AMF will likely limit the amount of resources available to plant communities, and thus limit the maximum plant biomass that can be achieved.

In conclusion, this study clearly shows that the composition of AMF communities alters the shape of the response curve between plant species diversity and productivity. The near ubiquitous presence of AMF in terrestrial ecosystems implies that production responses to declining plant diversity are likely to be more complex than plant-only studies have suggested.

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BIOSKETCH

John N. Klironomos' main research interest is in the ecology of soil organisms. In particular, he works on the influence of soil organisms on the functioning of terrestrial ecosystems, the use of soil microbes in landscape restoration, and the effects of global change on microbial diversity.

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