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Soil modification by different tree species influences the extent of seedling ectomycorrhizal infection

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Abstract Established vegetation can facilitate the ectomycorrhizal infection of seedlings, but it is not known whether this interaction is limited by the phylogenetic relatedness of trees and seedlings. We use a series of bioassay experiments to test whether soil modification by different ectomycorrhizal tree species causes different levels of seedling infection, whether the extent of seedling infection is a function of the relatedness of tree and seedling, and whether the effect of trees on seedlings is mediated by biotic or abiotic soil factors. We found that soils from under different tree species do vary in their mycorrhizal infectiveness. However, this variation is not related to the genetic relatedness of trees and seedlings but instead, appears to be an attribute of the overstory species, irrespective of seedling species, mediated through a suite of humus- and base-cation-related abiotic effects on soils. Modification of abiotic soil properties by overstory trees should be considered as an important factor in the effect of different overstory trees on the extent of seedling mycorrhizal infection.

Keywords Ectomycorrhiza · Facilitation · Seedling establishment · Mycorrhizal infection · *Quercus robur* · *Pinus sylvestris*

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Introduction

Established ectomycorrhizal vegetation can facilitate the probability or extent of ectomycorrhizal infection of seedlings by supporting mycorrhizal mycelium and increased local populations of mycorrhizal propagules, a process that we here term "mycorrhizal infection facilitation". There are many other possible interactions among plants via shared mycorrhizal mycelium (see reviews by Newman 1988; Simard and Durall 2004), including the possibility of carbon transfer (Simard et al. 1997), but mycorrhizal infection facilitation is an essential prerequisite for all further mycorrhizal interactions among plants: without seedling mycorrhizal infection, there can be no further mycorrhizal interactions among plants.

The ecological importance of tree influences on seedling mycorrhizal infection may be profound. Where ectomycorrhizal vegetation is absent, the establishment of ectomycorrhizal seedlings may be hindered by a lack of ectomycorrhizal inoculum (Marx 1991). In contrast, where ectomycorrhizal vegetation is present, the establishment of ectomycorrhizal plants may be facilitated (Dickie et al. 2002; Kranabetter 1999; Perry et al. 1989). This may lead to multiple steady states, with woodland openings and grasslands partially maintained by a lack of ectomycorrhizal inoculum (Dickie and Reich 2005; Terwilliger and Pastor 1999). Influences of ectomycorrhizal vegetation on the extent of infection of seedlings may persist for some time following disturbance as disturbances such as logging appear to relatively have minor effects on the extent (as opposed to community composition) of seedling infection (Jones et al. 2003), although the source of seedling infection may become increasingly dominated by fungal spores and sclerotia as opposed to vegetative mycelium (Baar et al. 1999; Stendell et al. 1999).

Mycorrhizal interactions among distantly related plants may be of particular ecological interest, as this may permit early successional plants to facilitate the establishment of later successional groups (Borchers and Perry 1987; Dickie et al. 2004; Horton et al. 1999). However, host-specificity of ectomycorrhizal fungi may limit the degree to which

established vegetation facilitates the mycorrhizal infection of seedlings (Molina et al. 1992). Most prior studies of mycorrhizal infection facilitation have only examined a very limited number of species combinations so that the influence of plant relatedness on mycorrhizal infection facilitation is not presently known.

A second limitation of prior studies has been that changes in mycorrhizal infection of seedlings planted near ectomycorrhizal vegetation have been assumed to be due to direct effects of established vegetation on the soil biota (particularly mycorrhizal inoculum). Alternatively, different tree species may indirectly influence seedling mycorrhizal infection by altering soil properties such as humus, soil pH, or soil nutrient availability, all of which are known to influence mycorrhizal fungal communities (Antibus and Liken 1992; Avis et al. 2003; Baar and deVries 1995; Baar et al. 1994; Conn and Dighton 2000; Kernaghan et al. 2003; Koide et al. 1998), or by differential shading of seedlings. Although shading can be controlled by careful placement of seedlings relative to sun exposure (e.g., Dickie et al. 2002), few, if any, studies have controlled for changes in soil abiotic conditions associated with established vegetation.

In the present study, our first objective was to determine the effect of plant relatedness on mycorrhizal infection facilitation, testing the hypotheses that:

(1) There are species-specific effects of established ectomycorrhizal plants on seedling mycorrhizal infection via soil modification.
(2) The more closely related established plants and seedlings are, the greater the degree of mycorrhizal infection facilitation.

Our second objective was to determine whether soil modification by established vegetation influences seedling infection primarily by biotic or by abiotic pathways. Our hypotheses were:

(3) Differences in the effect of different established plant species on the mycorrhizal infection of seedlings are due to changes in soil biota.
(4) Differences in the effect of different established plants on the mycorrhizal infection of seedlings are due to changes in soil abiotic properties.

Hypotheses 3 and 4, while different mechanisms for the same phenomenon, are not strict alternatives, as both can simultaneously be true.

Methods

Study system

For these studies, we used two seedling species (*Quercus robur* L. and *Pinus sylvestris* L.) and different subsets of overstory species from a unique set of 32- to 33-year-old replicated monocultures of 14 forest tree species at the Siemianice Experimental Forest in Central Poland (51° 14.87′N, 18°06.35′E, altitude 150 m). Twelve of the 14 tree species were ectomycorrhizal, including both conifers (*Abies alba*, *Larix decidua*, *Picea abies*, *Pinus nigra*, *P. sylvestris*, and *Pseudotsuga menziesii*) and angiosperms (*Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Q. robur*, *Quercus rubra*, and *Tilia cordata*), and two species were arbuscular-mycorrhizal (*Acer platanoides* and *Acer pseudoplatanus*). Although *Acer* has been listed as also potentially forming ectomycorrhiza (Smith and Read 1997), trypan-blue staining of roots from the site found no evidence of ectomycorrhizal infection (B. Kieliszewska-Rokicka, personal communication). The site was a mature *P. sylvestris* stand before clearing and planting in 1970–1971. The 14 tree species were planted in two adjacent sites, with each site having three replicates of nine species planted at 1×1 m spacing in 20×20 m plots; four species (*L. decidua*, *P. abies*, *P. menziesii* and *Q. robur*) were shared between the two sites (hence, these species are replicated six times). Stand closure had occurred in all plots, and some self-thinning has occurred. A more detailed site description is given in Withington et al. (2003). These sites have been extensively studied in an ongoing study of tree influences on soil physical and chemical properties, including measurements of soil pH, nutrients, base cations, calcium, texture, and numerous other variables for multiple depths (Reich et al. 2005).

Experiment 1: field planting

The objective of Experiment 1 was to test hypotheses 1 and 2 under field conditions. *Q. robur* acorns were collected in 2000 from mature trees growing at the Forest District, Kostrzyn, Poland, and stored for 2 years in a specialized seed storage facility in Jarocin. Acorns were planted in plots with *A. pseudoplatanus* (three plots), *C. betulus* (three), *F. sylvatica* (three), *L. decidua* (six), *P. abies* (six), *P. sylvestris* (three), *P. nigra* (three), *Q. robur* (six), *Q. rubra* (three), and *T. cordata* (three). In species with three replicate plots, we planted 18 acorns; 11 acorns were planted in species with six replicate plots. Acorns were sowed at a 2- to 3-cm depth. We also planted seeds of *P. sylvestris*, collected in December 2002 from the Forest District, Gniezno, Poland, but no seedlings successfully established. The same seed sources were used for all experiments.

Common methods for soil bioassays in Experiments 2, 3, and 4

Experiments 2, 3, and 4 were conducted under controlled shade–house conditions (50% of full sunlight reduction), using soil bioassay techniques (intact soil cores for Experiment 2, mixed sterile and unsterile soils for Experiments 3 and 4) in 2-l pots. Bioassays have the disadvantage of severing possible hyphal linkages between trees and seedlings (potentially reducing the opportunities for interactions), as well as the inevitable loss of realism in any more controlled experiment. Nonetheless, they also per-

mit removing any differences in shading or aboveground herbivory caused by different overstory species and also permit more careful monitoring and care of seedlings.

Experiment 2: soil bioassay

The objective of Experiment 2 was to test hypotheses 1 and 2. Both *Q. robur* and *P. sylvestris* seeds were planted in Experiment 2. Soil treatments were selected to obtain multiple levels of genetic relatedness. *Q. robur* seeds were planted into soils from *Q. robur*, *Q. rubra*, *F. sylvatica*, *C. betulus*, *T. cordata*, *L. decidua*, *P. sylvestris*, and *P. abies* plots as ectomycorrhizal treatments (in rough order of relatedness), and *A. pseudoplatanus* as an arbuscular mycorrhizal treatment. *P. sylvestris* seeds were planted into soils from *P. sylvestris*, *P. nigra*, *L. decidua*, *P. abies*, *Q. robur*, and *T. cordata* soils, with *A. pseudoplatanus* as an arbuscular mycorrhizal treatment. Soil monoliths were excavated intact and placed directly into 2-l pots between 17 and 19 May 2003. In each pot, three or five seeds were planted for the *Quercus* and *Pinus* bioassays, respectively. Each soil type (soil from beneath given tree species) was represented by 12 or 18 pots, depending on whether there were three or six plots available.

Experiment 3: different inoculum, common soil

The objective of Experiment 3 was to test hypothesis 3, that the effect of different established plant species on the mycorrhizal infection of seedlings was due to changes in soil biota. We planted *P. sylvestris* seeds in a mixture of five different soils (*P sylvestris*, *P. nigra*, *P. abies*, *Q. robur*, and *A. pseudoplatanus*), in which four of the five soils were sterilized. By varying which soil was not sterilized, we were able to hold the abiotic soil properties relatively constant while varying the source of soil biota. Soils were collected from a 0- to 20-cm depth and sterilized on three consecutive days, 40 min at 121°C on days 1 and 2, and 30 min at 121°C on day 3. Seeds were surface-sterilized with 30% H_2O_2 for 30 min prior to sowing five seeds in each pot. There were 12 replicates of each treatment. All seeds were sown on 10 June 2003.

Experiment 4: common inoculum, different soils

The objective of Experiment 4 was to test hypothesis 4, that the effect of different established plant species on the mycorrhizal infection of seedlings was due to changes in soil abiotic properties. Pots were filled with mixtures of 80% sterilized soil from each of the five species in Experiment 3 and 20% nonsterilized *P. sylvestris* soil as a source of ectomycorrhizal inoculum. The number of replications and all other methods were the same as in Experiment 3. All seeds were sown on 10 June 2003.

Originally, *Q. robur* seeds were also planted in both Experiments 3 and 4 (with *Q. robur*, rather than *P. sylvestris*, soil used as inoculum in Experiment 4), but ectomycorrhizal infection of the oaks, while present, was too poorly developed to allow accurate quantification.

Harvests and measurement of infection (all experiments)

All experiments were harvested between 23 and 26 September 2003. Roots were washed, and fine roots were severed from the taproot for measurement of ectomycorrhizal infection. Mycorrhizal infection was measured by a single researcher (I.A.D.) using a stereo microscope (4–40× magnification), with root tips of uncertain examined under a compound microscope for presence of Hartig net and mantle. All roots were placed in a Petri dish, and either 50 or 100% of root tips were measured on each seedling (using alternating squares on a grid for subsampling), with an average of 187 root tips counted per seedling.

In the present experiment, we did not attempt to identify ectomycorrhizal root tips to species. Existing molecular and morphology-based techniques for the identification of mycorrhiza require extensive database development specific to each study site and were therefore not practical for the present study. Mortality during the study had also reduced replication to the point that, given the high variability of fungal communities, we were unlikely to have sufficient statistical power to detect any possible shifts in the fungal community.

Statistics

Data were analyzed as analyses of variance (ANOVAs), using the aov procedure of R (version 2.0.0, R Foundation for Statistical Computing, Vienna, Austria), with Tukey's HSD used for means separation. In Experiments 1 and 2, to account for between-plot variation in soil characteristics, we performed statistical tests after removing variance that can be explained by soil texture. In extensive measurements of plot characters at these sites, only soil texture has been found to systematically vary as a function of location (Reich et al. 2005). Best-subset regression was used in Experiment 2 to determine which, if any, soil variables influenced ectomycorrhizal infection, with the lowest Bayesian information criterion (BIC) used to determine the optimal number of variable to include in the models.

Results

Experiment 1: field planting

There was high failure to germinate, and high mortality in the field planting, with no pine seedlings surviving and

only 51 oaks, in total, surviving. There was no significant effect of overstory species on oak survival (P=0.16). We present the mycorrhizal infection of the oak seedlings (Fig. 1) as a baseline for the bioassays, but results from the field were not significant (P=0.3), as might be expected given the low final replication and high variance.

Experiment 2: soil bioassay

Both oak and pine seedlings had significant differences in mycorrhizal infection as a function of soil origin (species of tree), supporting hypothesis 1. Hypothesis 2, that mycorrhizal infection would be greater under closely related species than under distantly related species, was not supported. *Quercus* seedlings had high infection in soils from under *Fagus* and *Larix*, low infection in soil from *Acer* and *Picea*, and intermediate infection under other treatments (Fig. 2a, P=0.0008). *P. sylvestris* seedlings also had high infection in soils from *Larix* plots and had low infection in soils from *Picea* and *P. nigra* plots, with intermediate infection in other treatments (Fig. 2b, P=0.0067). There were some similarities between the *Quercus* bioassays and the field results, in that seedlings in *Fagus* and *Larix* soils which had high infection in the bioassay also had relatively high infection in the field results, while seedlings in *Acer* and *Picea* soils had relatively low infection in both experiments.

There were similarities in the high ectomycorrhizal infection of *Pinus* and *Quercus* seedlings in bioassay soils from the *Larix* plots and the low levels of infection in soils from the *Picea* plots for both seedling species. We did a post hoc test of the correlation of results across overstory species plots weighted by sample sizes and confirmed that

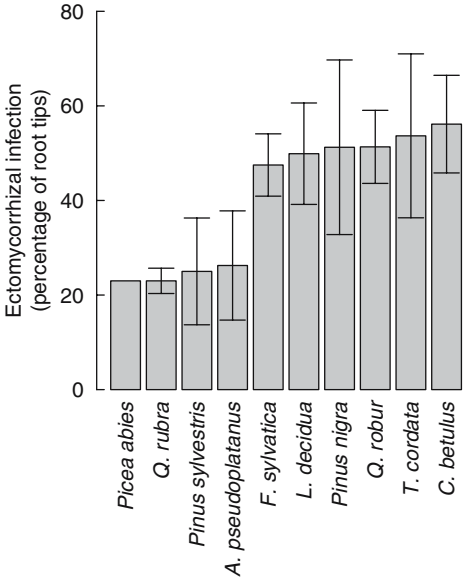

Fig. 1 Ectomycorrhizal infection of oak seedlings in Experiment 1 (field planting) as percentage of total root tips. *Error bars* are 1 SE, n=1 for *Picea abies*. Differences between treatments are not significant

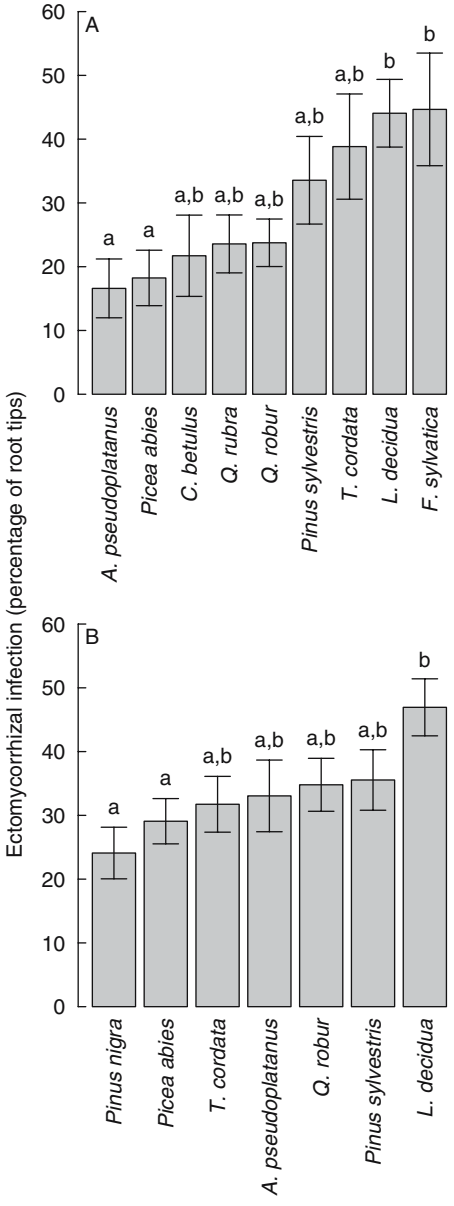

Fig. 2 Ectomycorrhizal infection in Experiment 2 (soil bioassays) for *Quercus robur* (**a**) and *Pinus sylvestris* (**b**) seedlings in soils from under different overstory tree species. *Error bars* are 1 SE; *bars with different letters* are significantly different at P<0.05 (Tukey's HSD)

there was a significant relationship (P=0.035, r^2=0.17). The similarity of results between *Quercus* and *Pinus* bioassays provides further evidence refuting hypothesis 2.

In best-subset regression of percent infection as a function of soil variables, *Q. robur* seedling infection was best described (lowest BIC) by humus percent carbon, humus cation exchange capacity, and soil percent base saturation at 20- to 40-cm depth (P<0.0001, r^2=0.25); *P. sylvestris* seedling infection was best described by humus percent N (total), soil Ca from 20 to 40 cm depth, soil percent clay, and soil cation exchange capacity at 0- to 20-cm depth (P<0.0001, r^2=0.21). Overstory species was never included in the lowest BIC model and was never included among any best-subset model with up to eight predictor

variables. In addition, there was no longer any significant effect of overstory species on the extent of seedling infection after accounting for soil properties using the lowest BIC model. This is consistent with hypothesis 4, that differences in the effect of different established plants on the mycorrhizal infection of seedlings are due to changes in soil abiotic properties. The lack of any residual overstory effect after accounting for soil variables provides some evidence against hypotheses 2 and 3.

Aboveground biomass of *Q. robur* was significantly positively correlated with mycorrhizal infection ($P<0.001$, $r^2=0.17$, not shown) and not significantly affected by overstory species ($P=0.15$). Aboveground biomass of *P. sylvestris* was weakly, but significantly, negatively correlated with ectomycorrhizal infection ($P=0.0046$, $r^2=0.04$) and significantly influenced by overstory species ($P=0.024$, Fig. 3), with low growth in the soils from the *P. nigra* stands and high growth in soils from the *T. cordata* stands.

Experiment 3: different inoculum, common soil

In the common soil experiment, *P. sylvestris* seedlings, planted into a common soil with five different inoculum sources had 20–40% of root tips infected but showed no significant variation in ectomycorrhizal infection as a function of inoculum source ($P=0.48$). There was therefore no support for hypothesis 3, that overstory effects were due to changes in soil biota.

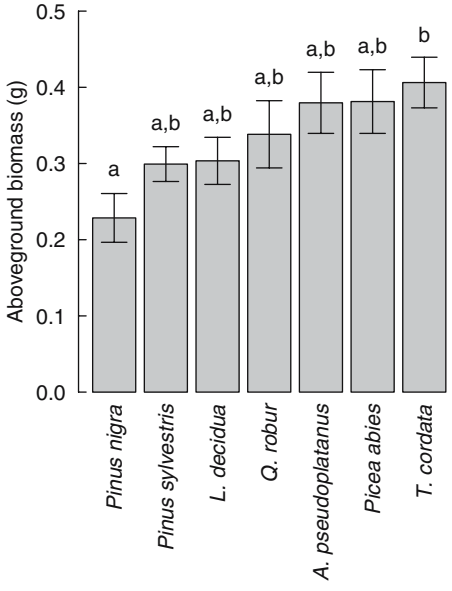

Fig. 3 Aboveground biomass of *P. sylvestris* seedlings as a function of soil source in Experiment 2 (soil bioassays). *Error bars* are 1 SE, *bars with different letters* are significantly different at $P<0.05$ (Tukey's HSD). Biomass of *Q. robur* (not shown) was not significantly affected by soil source

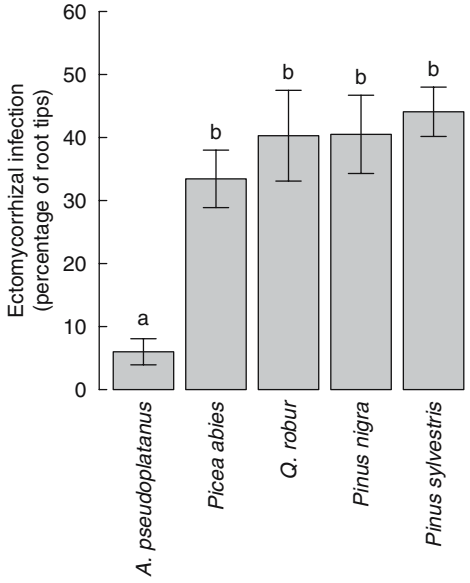

Fig. 4 Ectomycorrhizal infection of *P. sylvestris* seedlings as a function of abiotic soil properties in Experiment 4 (common inoculum, different soils). *Error bars* are 1 SE, *bars with different letters* are significantly different at $P<0.05$ (Tukey's HSD)

Experiment 4: common inoculum, different soils

Pinus sylvestris seedlings planted into sterilized soils from under five overstory species reinoculated with a common inoculum showed significant variation in mycorrhizal infection, with very low infection in *Acer* soils and high infection in other soils (Fig. 4, $P<0.001$). This provides limited support for hypothesis 4, although the only significant difference was between soil from under an arbuscular-mycorrhizal tree compared with soils from under ectomycorrhizal trees.

Discussion

Significant variation in the extent of seedling mycorrhizal infection did occur as a function of overstory species (supporting hypothesis 1, that mycorrhizal infection would depend on the species of a surrounding plant), but there was no evidence that this was a function of the relatedness of established plants and seedlings (refuting hypothesis 2). Instead, the significant correlation of results from *Pinus* and *Quercus* seedling bioassays suggests that the effect of trees on the extent of seedling ectomycorrhizal infection is a function of the overstory species alone regardless of seedling species.

Two lines of evidence suggest that abiotic soil modification was a major determinant of seedling mycorrhizal infection. From best-subset regression of the bioassay results, a suite of base-cation- and humus-related soil traits were the best predictors of seedling infection, with no residual effect of overstory species. In addition, there was no influence of inoculum source on *Pinus* seedling infection in a common soil in Experiment 3, but there were

significant effects of abiotic soil properties on *Pinus* seedling infection with a common inoculum in Experiment 4. These results are consistent with prior observations of the sensitivity of mycorrhizal infection to changes in soil humus and organic matter (Baar and deVries 1995; Conn and Dighton 2000; Jones et al. 2003; Koide et al. 1998), pH (Bakker et al. 2000), nutrients (Avis et al. 2003; Lilleskov et al. 2002), and overstory composition (Kernaghan et al. 2003).

The effect of different overstory trees on seedling growth may depend on a number of factors. In the bioassays, *Q. robur* biomass was positively correlated with ectomycorrhizal infection, suggesting that tree species that increase seedling infection will tend to increase seedling growth. In contrast, *P. sylvestris* biomass was weakly negatively correlated with ectomycorrhizal infection and was lowest in soil from under *Pinus* trees and highest in soils from less related trees (particularly *Tilia* soils). This suggests that nonmycorrhizal soil-mediated influences of trees on seedlings, perhaps through the modification of soil characteristics or increased populations of host-specific pathogens, may have played an important role in influencing *P. sylvestris* seedling growth.

Facilitation of mycorrhizal infection can clearly occur when seedlings are planted near established ectomycorrhizal vegetation or in soil from under established plants, and may influence seedling growth, as seen in the present study and in a number of prior studies (Borchers and Perry 1987; Dickie et al. 2002; Kranabetter 1999). Results from the present study suggest that indirect effects of established vegetation on seedlings via modification of abiotic soil variables may be an important driver of changes in the extent of seedling mycorrhizal infection. The relatedness of trees and seedlings did not appear to be an important factor in the extent of seedling infection. We did not examine the diversity or species composition of seedling infection, but prior studies suggest that these variables may be more affected by tree and seedling relatedness than the extent of infection per se (Kranabetter 1999).

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