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Thuja plicata exclusion in ectomycorrhiza-dominated forests: testing the role of inoculum potential of arbuscular mycorrhizal fungi

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Abstract The ability of trees dependent on arbuscular mycorrhizal (AM) fungi to establish in ectomycorrhizal forests is unknown. On northern Vancouver Island, Canada, there are sharp boundaries between mixed red cedar (*Thuja plicata*)-hemlock (*Tsuga heterophylla*) (CH) stands, and stands of hemlock and amabilis fir (*Abies amabilis*) (HA). We tested differences in AM colonization of red cedar between ectomycorrhiza-dominated (HA) stands and stands containing red cedar (CH), across a range of light levels. We used a soil bioassay approach to determine whether there was sufficient AM fungal inoculum in the HA tree stands to colonize red cedar seedlings. Seeds of hemlock and red cedar were sown in forest floor samples collected from the two types of forests, and shade treatments ranging from <1 to 53% of full sunlight were imposed. After 6 months, seedling survival and root and shoot biomass were quantified, and red cedar seedlings were sampled for AM fungal colonization. Hemlock survival and growth did not differ between soil types, suggesting there was no substrate-associated limitation to its establishment in either forest type. Red cedar colonization by AM fungi was significantly correlated with light levels in CH soils but arbuscular mycorrhizas were absent in roots of red cedar seedlings grown in HA soil. Red cedar survival and relative growth rate were significantly greater in the CH than in HA soil; higher growth was due primarily to greater shoot growth in CH soils at high light levels. The low soil inoculum potential for red cedar in ectomycorrhiza-dominated stands may account for the virtual exclusion of red cedar seedlings from these forests.

Keywords Climate change · Colonization · Dispersal · Shade · Tree distribution

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Introduction

Interest in the potentially important role that mycorrhizal fungi play in influencing plant community membership and diversity has recently increased (Francis and Read 1994; van der Heijden et al. 1998a,b; Hartnett and Wilson 1999; O'Connor et al. 2002). Arbuscular mycorrhizal (AM) fungi can alter the relative performance of plants (Kough et al. 1985; Klironomos 2003), and can affect diversity by changing dominance relations among plant species (Hartnett and Wilson 1999; Urcelay and Diaz 2003). Typically, species comprising the main structural components of the vegetation in a given ecosystem are colonized by the same group of mycorrhizal fungi. In the northern hemisphere arbuscular mycorrhizal plants tend to dominate in relatively mild climates and in low phosphorus soils, whereas ectomycorrhizal plants dominate in colder climates and in soils of high organic matter and low nitrogen (Read 1991; Allen et al. 1995). In zones where the two groups overlap, the interaction between ecto- and AM tree communities is poorly understood. Of the little research performed on this topic, most has occurred in tropical areas where local patches of ectomycorrhizal trees occur within predominantly arbuscular dominated forests (Alexander 1989; Moyersoen et al. 1998; Onguene and Kuyper 2002). Within North America, laboratory and field studies have shown that the absence of AM inoculum restricts AM plant establishment in the understory of live ponderosa pines, an ectomycorrhizal tree species (Kovacic et al. 1984). Similarly, a lack of

ectomycorrhizal fungi limited conifer invasion into beaver meadows (Terwilliger and Pastor 1999). Although few in number, results from these studies suggest ectomycorrhizal communities are mutually exclusive of AM communities and vice versa.

With current predicted movements of plant communities in response to changing climatic conditions (Overpeck et al. 1991; Parmesan and Yohe 2003), it is critically important to understand the interactions between ecto- and AM communities in more northern areas. As warmer conditions develop in more northern areas, more southern, typically AM trees will no longer be limited by climatic barriers. Thus, there will likely be an increase in interactions between AM and ectomycorrhizal communities. However, both symbionts, AM fungi and tree host, must be able to arrive and establish in what is currently predominantly ectomycorrhizal forests.

Northern Vancouver Island, off the west coast of Canada, offers an interesting case study of the interaction between ecto- and arbuscular mycorrhizal tree communities. Western red cedar (*Thuja plicata* Donn.), a species associated with arbuscular mycorrhizas, began establishing approximately 3,000 years ago in a forest dominated by ectomycorrhizal Sitka spruce [*Picea sitchensis* (Bong.) Carrière], western hemlock (*Tsuga heterophylla* Raf. Sarge) and amabilis fir (*Abies amabilis* Dougl.) (Hebda 1983). The current landscape reflects this historical influence, with two distinct forest types occupying mesic sites: the hemlock-amabilis fir (HA) and the red cedar-hemlock (CH) forests (Lewis 1982). These forest types tend to have clear boundaries with little or no red cedar regeneration inside HA stands (Prescott and Weetman 1994; Weber et al. 2003), but abundant hemlock regeneration in both stand types. Researchers have attempted to explain the exclusion of red cedar from HA stands based on shade tolerance (Weber et al. 2003) and disturbance history (Prescott and Weetman 1994). Although the processes responsible for maintaining two distinctive forest types on apparently similar sites are not fully understood, initial research suggests that red cedar is excluded from HA stands by an interaction between low light and an incompatibility with the HA substrate (Weber et al. 2003). Measurements taken within intact CH and HA stands showed that soil chemical or physical properties were not substantially different among the two stands; mineral soils in CH stands had lower amounts of total N, but were similar with respect to organic C, C:N, available P, aluminium, and soil texture (De Montigny 1992; reviewed in Prescott and Weetman 1994). However, samples of the forest floor layers [litter (L), fermentation (F) and humus (H)] of the two different stands showed a different trend where concentrations of total and extractable N and P, and mineralized N were lower in the CH than those in the HA (Prescott et al. 1993).

There is low species richness and abundance of understorey vascular plants in these two forest types, with such plants in HA stands typically covering 0 to 3% of the forest floor (Weber et al. 2003). These plants consist mostly of ericaceous shrubs, several species of orchids and ferns, and of these only ferns, which are a minor component of the flora, are regarded as putative hosts to AM fungi. In neither of these forest stands do all understorey plants and trees show fidelity to the same type of mycorrhizal associations. Compatibility with multiple types of mycorrhizal associations (e.g. among ericoid, orchid, arbuscular or ectomycorrhizal fungi) is uncommon within a single host species (Molina et al. 1992). Therefore, candidates of potential inoculum for any particular host species will be restricted, but the availability of the inoculum will vary depending on the mycorrhizal status of the surrounding vegetation. For example, within these forests ectomycorrhizas are found in a variety of common tree species. Consequently, when one tree species is removed from the stand, root systems of other tree species can act as sources of ectomycorrhizal fungal inoculum. Western red cedar, an obligately AM species (Curran and Dunsworth 1988), is the only AM tree species within these forests. It has been shown to react more positively to inoculation with AM fungi than other closely related tree species (Kough et al. 1985). Therefore, it is likely that establishment of western red cedar is severely limited where there are no other sources of compatible AM inoculum.

This study was designed to investigate the hypothesis that limitations in AM fungal inoculum in HA stands may be responsible for red cedar exclusion. The absence of critically required symbionts could account for the poor survival and growth of red cedar seedlings. Due to the potentially confounding effects of light availability in a forest understory, we also examined the consistency of AM fungi-red cedar relationships across a range of light levels. We performed a greenhouse soil bioassay using forest floor materials collected from CH and HA sites to address the following questions: (1) Do red cedar seedlings show differences in survival and growth between the substrates? (2) Does substrate determine the probability that AM fungi will colonize red cedar? (3) Are differences in colonization and red cedar performance consistent across a range of light levels? (4) How do these results for red cedar compare to those for hemlock, which is known to establish in both forest types?

We used the soil bioassay approach to quantify the inoculum potential in the two stand types. Inoculum potential is defined as the capacity of mycorrhizal fungal propagules to form associations with roots in a particular soil and can be measured by the rate of colonization of host roots. Counting propagules or indirect estimates do not always correspond with mycorrhiza formation in soil (Abbott and Robson 1991; Brundrett 1991). Therefore, soil bioassays that measure mycorrhiza formation on red cedar seedlings grown in soil samples are expected to provide a better estimate of inoculum potential for this species (Brundrett and Abbott 1994). The effects of inoculum potential on red cedar seedling recruitment within the forest stands were assessed by

measuring growth and survival of seedlings. Including hemlock as an additional bioassayed species allowed for differences associated with other chemical, physical or non-AM factors between CH and HA substrates to be detected.

Materials and methods

Forest floor samples were collected from 12 to 14 May 1999 from four areas containing both CH and HA forest types. Intact forest floor was collected to 50 cm depth and put into garbage bags. The soil collection sites range in distance from approximately 5 to 15 km, and were located within the Port McNeill forest area on northern Vancouver Island, Canada. Once shipped to the University of British Columbia, Vancouver, the samples of each forest type were mixed by hand, and coarse twigs, large sticks and leaves were removed. The soil was stored in a cool, open area until 28 May, and afterwards samples from each site type were combined and the composite samples for each forest type were transferred to pots. Red cedar and stratified hemlock seeds from the BC Tree Centre (seedlots 60218 and 06891, respectively) were germinated on filter paper and then planted into 3.7 l pots containing either CH or HA forest floor on 29 May 1999. A total of 160 pots were placed in a greenhouse on the University of British Columbia campus (Vancouver, British Columbia), and were left under ambient light (approximately 54% of full sunlight). After 6 days, pots of each substrate type were randomly assigned to a shade treatment. Forty shade houses were constructed with three densities of neutral shading cloth applied in one, two or three layers to produce nine shade treatments (3 densities ×3 numbers of layers). A tenth treatment of ambient light was also included, and positioning of these treatments within the greenhouse was randomly assigned. In total, there were four treatments (2 species ×2 substrates), ten light regimes, and four replicates of each for a total of 160 pots. The experimental design was a randomized split-plot, with each species by substrate combination housed within a light treatment. Light measurements were done in the greenhouse to assess actual light levels within each shade treatment and the actual light levels were used in all analyses. All light measurements were taken using two calibrated Decagon sunfleck ceptometers, following the protocol of Parent and Messier (1996).

Pots with high germinant mortality in the first week were replanted so that the minimum number of initial seedlings was at least 5 per pot. Initial germinant numbers were recorded as those surviving on June 12. Seedling survival per pot was recorded on November 19, slightly less than 6 months after the initial planting. Pots were put in a dark cold-room (temperature approx. 2°C) on 28 November 1999, and plants were harvested from 29 November to 1 March 2000. Roots and shoots of both species were separated and dried at 74°C overnight, and weighed. Roots of 66 red cedar seedlings were used to create dry-to-wet-weight regressions, with three separate regressions developed for different drying times required for different root sizes (r^2 values ranged from 0.98 to 0.997). These regressions were used to predict the dry weight of roots sampled for mycorrhizas. Roots from three red cedar plants were taken from each red cedar pot to test for AM colonization. Red cedar roots that were sampled for mycorrhizas were cleared and stained by Dr. G. Xiao at the University of British Columbia, and then assessed for presence of arbuscular mycorrhizas. For each seedling the entire root length was examined for presence of AM with a dissecting microscope and questionable observations were confirmed by use of a compound microscope. If vesicles, arbuscles or AM hyphae were observed at any point along the length of the root, the seedling was considered to be mycorrhizal, thus negating any effects of internal hyphal spread within a root system.

Statistical analyses

Analyses of covariance (ANCOVA) were used to test the effects of treatments on relative growth rate and survival, with the light treatment included as the continuous variable and the substrate and species included as class variables. For all ANCOVA tests, the light by replicate error term was used to test the effect of light, and the residual error term was used to test the class variables and interaction terms. The relative growth rate (RGR) of each individual was calculated as: RGR = ln (total dry weight)−ln (seed mass) with time consistent for all plants (184 days). Seed masses of red cedar and hemlock were 1.36 and 2.40 mg/seed, respectively. RGR was averaged within each experimental unit prior to ANCOVA and permutation tests. Light levels were log transformed in both analyses, and survival was arcsine transformed to improve the normality of the data distributions (Neter et al. 1996).

Survival was tested with a logistic model (binomial distribution) using PROC Genmod in SAS system 8.02 (SAS 1999). Results from this test were identical to those from a linear model with survival rate arcsine transformed; the latter test is reported due to the simplicity of interpretation. Both the RGR and survival analyses had significant interaction terms (non-parallel slopes), with the RGR containing a three-way interaction (light × substrate × species) and the survival analysis containing a two-way interaction (species × substrate) (Table 1). Therefore, each analysis was subsequently tested for differences between substrate types for each species to obtain specific responses to the treatments. Permutation tests were used to test for differences in slope and intercept (following Kleinbaum and Kupper 1978), with the (x,y) pair randomly assigned to either treatment. Thus the null population consisted of the combined observations from both treatments, and the slope and intercept were simultaneously generated to develop the

Table 1 Type 3 analysis of covariance (ANCOVA) results for *T. plicata* survival and RGR analyses

Source	*df*	Survival *F*	Survival $P > F$	RGR *F*	RGR $P > F$
Light[a]	1	16.58	< 0.0001	155.49	< 0.0001
Substrate	1	11.73	0.0009	0.28	0.5982
Species	1	17.36	< 0.0001	13.55	0.0004
Species × substrate	1	5.62	0.0194	1.99	0.1614
Light × species	1	0.56	0.4546	0.17	0.6835
Light × substrate	1	0.74	0.39	0	0.9476
Light × species × substrate	1	0.03	0.8532	9.67	0.0025

[a]The light term was tested with the light × replicate interaction term, and the remaining terms were tested with the residual variance

null distributions of both parameters. A total of 9,999 permutations were run for each test. ANCOVA was also done on log-transformed shoot and root masses. The shoot analysis showed a three way interaction, and species were subsequently tested with permutation tests as with the RGR and survival analyses.

We performed an additional analysis to ensure that pots with more seedlings surviving did not show lower growth due to competitive interactions (i.e. we tested for this experimental artefact). Residuals from a covariate analysis regressing light versus growth for both cedar and hemlock showed no relationship with the number of seedlings remaining in a pot ($r^2 < 0.02$).

Probability of colonization of red cedar germinants by AM fungi was tested using a logistic regression with light as the independent variable and each pot serving as an observation. The logistic regression, dry weight regressions and covariance analyses were done using SAS system 8.02 (SAS 1999), and the permutation tests were constructed and run using Visual Basic.

Results

Colonization of red cedar roots by AM fungi was significantly related to light levels in the CH soil ($P < 0.015$, Fig. 1), with the predicted and observed values showing a good fit (81.4% concordant, 14% discordant and 4.6% tied). Colonization of red cedar in CH soil was observed at irradiances greater than 10% of full sunlight. In contrast, only one red cedar germinant in the HA soil treatment became colonized; therefore irradiance and colonization were not correlated.

Survival of hemlock was positively correlated with light levels for both substrate treatments ($P < 0.001$; Table 1), but did not differ significantly between substrates. Likewise, red cedar survival was correlated with irradiance, but was significantly greater in the CH than in the HA soil (21% difference in intercept, $P < 0.05$). Slopes did not differ between substrates (Fig. 2). The difference in intercept with no significant difference in slope indicates that survival was higher on average in the CH at all light levels.

Relative growth rates of hemlock did not differ significantly between substrate treatments; however, the RGR of red cedar was significantly higher in the CH than the HA soil ($P < 0.05$, Fig. 3). The difference in the intercept was not statistically significant ($P = 0.056$). The greater slope and similar intercept indicate that red cedar RGR was similar between HA and CH substrates at low light, but that as the amount of light increased, red cedar grew more quickly in CH soil.

To better understand the difference in RGR between the species within each substrate, we examined the masses of roots and shoots separately. Growth of hemlock roots and shoots was not influenced by substrate. Redcedar showed a significant difference in shoot growth between substrates (Fig. 4), with a lower inter-

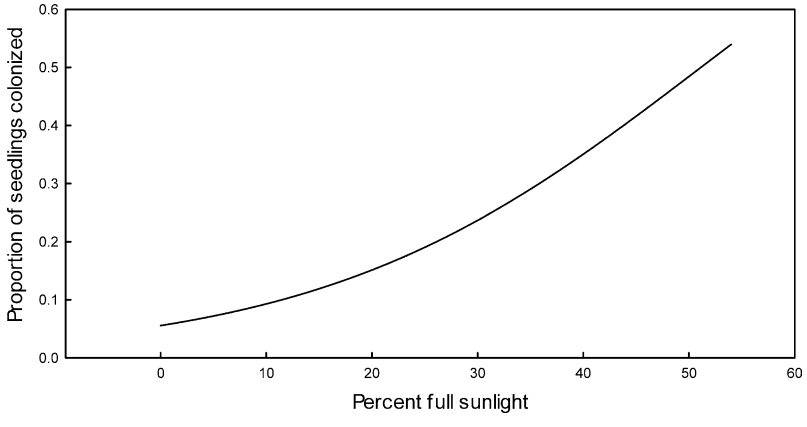

Fig. 1 Proportion of *Thuja plicata* seedlings colonized by arbuscular mycorrhizal fungi in substrates from *T. plicata*-dominated (CH) stands as modeled by logistic regression ($P < 0.015$)

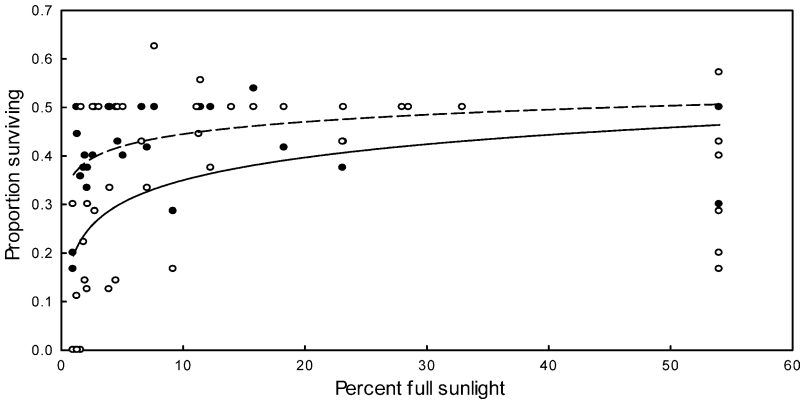

Fig. 2 *T. plicata* survival in substrates from *T. plicata*-dominated (CH; *black circles*, *dashed lines*) and *T. heterophylla*-dominated (HA; *open circles*, *solid lines*) ecosystems. Analysis was performed on arcsine transformed units. Note: overlapping points show only *open circles*

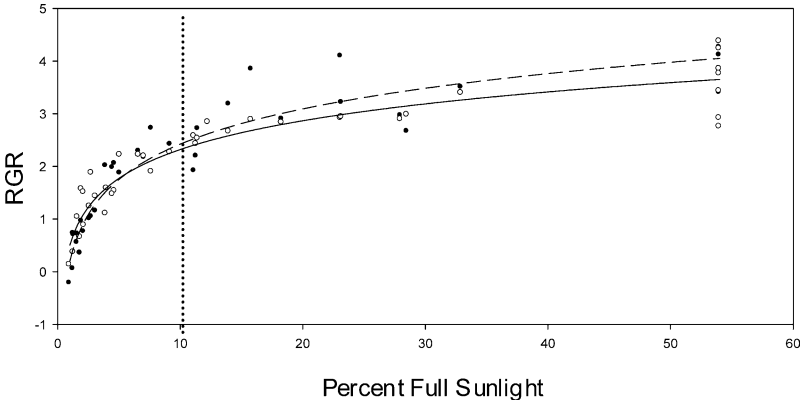

Fig. 3 *T. plicata* RGR in substrates from *T. plicata*-dominated (CH; *black circles*, *dashed lines*) and *T. heterophylla*-dominated (HA; *open circles*, *solid lines*) (HA; *open circles*, *solid lines*) ecosystems. RGR is given for the length of the experiment (approximately 6 months). The *dotted line* at 10% sunlight indicates the light level at which arbuscular mycorrhizal fungi began colonizing *T. plicata* in the CH

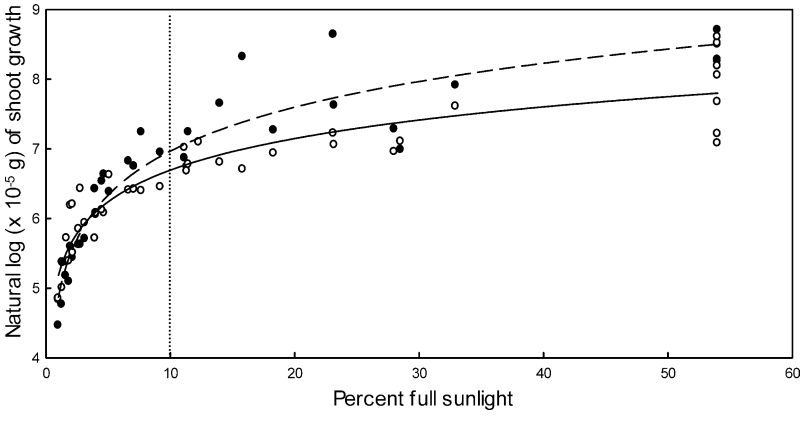

Fig. 4 *T. plicata* shoot growth (log transformed) in substrates from *T. plicata*-dominated (CH; *black circles*, *dashed lines*) and *T. heterophylla*-dominated (HA; *open circles*, *solid lines*) (HA; *open circles*, *solid lines*) ecosystems. The *dotted line* at 10% sunlight indicates the light level at which arbuscular mycorrhizal fungi began colonizing *T. plicata* in the CH

cept ($P < 0.05$) and steeper slope ($P < 0.001$) in the CH treatment. Thus at very low light levels, red cedar shoots grew more slowly in the CH than HA, but this difference disappeared at light levels commonly found within the forest (2.4% full light). At higher light levels, red cedar shoots grew more quickly in the CH than the HA. For example, at 10 and 40% full sunlight, shoots of seedlings grown in the CH had predicted masses of 1.3× and 1.9× that of seedlings grown in HA substrate. Red cedar roots showed no significant difference between substrate treatments.

Overall, none of the seedling characteristics of hemlock was significantly affected by soil type. In contrast, red cedar had lower survival in HA soils. At low light, red cedar shoots grew less in CH soils than HA soils, but this was countered by an increasingly higher growth rate with more light. Total RGR reflected similar patterns as red cedar shoots, but these were somewhat weaker be-

cause red cedar root growth was not affected by substrate type. The higher growth potential and survival of red cedar in CH soil was accompanied by AM fungal colonization.

Discussion

The relationship between increasing AM fungal colonization and growth with increasing light has been shown in plants such as onion (Hayman 1974), sudan grass (Ferguson and Menge 1982), tomatoes and maize (Daft and El-Giahmi 1978), and some tropical forest trees (Gehring 2003). We expected that with increasing light, red cedar seedling biomass and AM fungal colonization would increase. Red cedar seedlings grown in the CH substrate followed this prediction. When grown in the HA substrate, biomass, but not colonization, of red cedar seedlings increased with irradiance. This suggests either that there was a very low abundance of AM fungal propagules in the HA soil, or that colonization by existing AM propagules was inhibited. In either scenario, AM inoculum potential was low in the HA substrate. Inference of greenhouse results to field conditions should be performed with caution, as AM fungi assayed in this study will be a constrained pool of those species found in intact forests because species present via intact hyphal networks will be omitted. However, given the lack of apparent AM host species in the HA, greenhouse results may well reflect field conditions. The upper threshold of light treatments was well above the level experienced naturally in the forest (average light levels in intact forest range from 3.5 to 3.7%, and on forest edges from 32 to 37%, Weber et al. 2003); this, combined with the relatively large size of the redcedar seedlings in the high light treatments (Fig. 3), precludes the possibility that carbon limitation to the seedlings caused low colonization of arbuscular mycorrhiza in the HA.

Hemlock showed no differences in growth between the two substrates suggesting there were no other influential chemical or physical factors affecting growth or survival of seedlings. Red cedar showed greater growth, survival and AM colonization in the CH despite the generally lower levels of nitrogen found in this forest type (Prescott et al. 1993). In a similar pot assay of forest floor samples collected from the two stands, cedar seedlings had higher biomass in substrates collected from HA than CH stands (Prescott et al. 1993); however, no attempts were made to control for possible spore contamination of the samples and no assessment was made of mycorrhizal colonization of seedling roots. Without knowing the mycorrhizal status of these seedlings, comparing seedling growth may be misleading. In our study, given that AM colonization occurred in conjunction with higher red cedar growth and survival, we propose that colonization by AM fungi in part determines the success of red cedar seedlings in these forest stands.

Forest community composition implications

On the landscape scale, patches of CH stands containing AM tree communities are surrounded by ectomycorrhiza-dominated HA forests. Although plant species that form other types of mycorrhizal associations are present in HA stands, these plants are very sparse (Weber et al. 2003) and consist mainly of ericaceous shrubs, which do not host AM fungi. Red cedar and the other common tree species (hemlock and amabilis fir) are mutually exclusive with respect to their mycorrhizal fungal symbionts. Consequently, invading red cedar would not be able to connect into an existing mycorrhizal hyphal network or be colonized by fungal propagules of mycorrhizas of the other tree species. In this situation, connections to existing vegetation of the AM type or adequate dispersal of AM propagules become imperative for red cedar to regenerate.

In our experiment, growth and survival of red cedar seedlings was substrate-dependent and coincided with AM colonization. These differences were significant, with survival differing by 21% between soil types and growth of red cedar seedling shoots almost doubling when in CH substrates under light levels typical of those found at a forest edge. Spatial variation in AM fungi may give rise to spatial variation in seedling establishment and survival (Lovelock et al. 2003). Propagules of AM fungi are thought to include spores, dead root fragments, and networks of hyphae in soil but, relative to ectomycorrhizal fungi, propagules disperse over shorter distances. There are several reasons for this. First, the spores of AM fungi are much larger than spores of ectomycorrhizal fungi (100 μm or larger versus 10 μm, respectively) (Fitter 1992). Second, most AM fungal propagules disperse through passive movement within the soil (Brundrett and Abbott 1994, but see Allen and Macmahon 1988; Allen et al. 1992; Gehring et al. 2002) and AM do not have anastomosing hyphae, which are also much finer and smaller in extent than ectomycorrhizal mycelia (Miller and Allen 1992; Read 1992). Thus, robust mycelial connections covering a large area are not likely. Given limited dispersal by AM fungi, the clear boundaries between HA and CH stands and the lack of red cedar seedling success in HA stands may well reflect the pattern of AM fungi availability to red cedar seedlings. Indeed, our results suggest that red cedar appears to be limited by AM fungal availability, which in turn may be limited by appropriate hosts, such as red cedar. This constitutes a 'chicken and egg' problem that may limit considerably the spread of both red cedar and AM fungi. Alternatively, AM inoculum may be present in HA stands, but is inhibited by other factors in the soil. Untested in our study, we cannot rule this out as a possible explanation to explain poor red cedar recruitment in HA stands.

Assuming dispersal is insufficient for AM tree species, connecting to a hyphal network of AM fungi or other types of AM inoculum may be critical for red cedar seedling establishment. The only common understory

herb available as a possible AM fungi source in HA stands is deer fern (*Blechnum spicant*). However, the arbuscular status of pteridophytes is unclear and mycorrhizal dependency varies among pteridophyte taxa and regions (Cooper 1976; Gemma et al. 1992; Berch and Kendrick 1982; Zhi-wei 2000). The ability of ferns to act as vectors for AM fungi of seed plants is unknown and merits further study. In addition, there is increasing evidence that AM fungi are not host generalists (Helgason et al. 2002; Husband et al. 2002; Sanders 2002; Vandenkoornhuyse et al. 2003); hence, even if deer fern do host AM fungi, these AM fungi species may be incompatible with red cedar.

Unlike red cedar, hemlock seedlings grew equally well in either substrate. We did not measure inoculum potential of ectomycorrhizal fungi; however, it is evident that hemlock seedlings experienced no or equal inhibiting factors in the two different soil types, and/or any soil organisms necessary for seedling growth, such as ectomycorrhizal fungi, were equally accessible in both soil types. Dispersal of ectomycorrhiza propagules includes root fragments, hyphae and spores that are discharged into the air for wind dispersal (Molina et al. 1992). Additionally, due to hyphal anastomosis, ectomycorrhizal fungi form a net of mycelium stretching meters across a forest floor (Bergemann and Miller 2002; Kretzer et al. 2004). Many ectomycorrhizal fungi are multi-host compatible (Horton and Bruns 1998), and understorey vegetation can provide inoculum in periods where tree hosts are absent (Horton et al. 1999; Hagerman et al. 2001). The presence of hemlock trees in both stands suggests that hemlock seedlings become colonized either by joining existing hyphal networks in these stands, from long-lived soil inoculum, or from spores dispersed over long distances. Ectomycorrhizal species were present on the landscape prior to red cedar, implying that a priority effect also may have occurred; the ectomycorrhizal status of the pre-existing vegetation may have facilitated the current ectomycorrhizal species. This would clearly give ectomycorrhizal tree species an advantage over non-ectomycorrhizal plant species in terms of inoculum availability.

Mycorrhizas can be an important factor in determining the trajectory of succession within forests (Trappe 1989). Feedbacks between plant and soil communities have been cited as an underlying process shaping plant communities (Perry et al. 1989). Disruption of these feedbacks, as a result of severe disturbances such as clearcutting, may explain why changes in one community mirror changes of another. Once the composition of a community changes through the removal of essential organisms, the associated community may be difficult to restore. For example, Amaranthus and Perry (1987) and Borchers and Perry (1987) working in forests of the Pacific Northwest, reported that a lack of inoculum was an important factor in determining success of seedling regeneration [but see Jones et al. (2003) for a re-analysis of data from studies of this kind]. Indeed, many introduced *Pinus* species were unable to establish until the trees were inoculated with compatible ectomycorrhizal fungi (Reynolds et al. 2003). The disruption of both ectomycorrhizal and AM communities by large disturbances may facilitate changes in the aboveground community, and this deserves further study.

Given projected climate predictions, northward shifts in species ranges are expected (Overpeck et al. 1991; Parmesan and Yohe 2003). Historically, forests of northern climates have been dominated by ectomycorrhizal host species and AM plant communities have been found in temperate forests and grasslands (Moser 1967 in Allen et al. 1995). As southern plant communities move northward, landscape patterns may shift from being more or less mono-dominant ectomycorrhizal forests to a mosaic of arbuscular and ectomycorrhizal tree communities. Our study suggests that this transition is not simply a matter of plant establishment irrespective of their associated mycorrhiza. Arbuscular mycorrhizal fungi may be severely dispersal limited, and the spread of AM-dependent tree species may be limited by the dispersal of the fungi. Indeed, in ectomycorrhizal landscapes dispersal limitation in AM fungi may be equally or more important than dispersal limitation in their hosts.

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References

Abbott LK, Robson AD (1991) Factors influencing the occurrence of vesicular-arbuscular mycorrhizas. Agric Ecosyst Environ 35:121–150

Alexander IJ (1989) Mycorrhizas in tropical forests. In: Proctor J (ed) Mineral nutrients in tropical forest and Savannah ecosystems. Blackwell Scientific, Oxford, UK, pp 169–188

Allen MF, Macmahon JA (1988) Direct VA mycorrhizal inoculation of colonizing plants by pocket gophers (*Thomomys-talpoides*) on Mount-St.-Helens. Mycologia 80:754–756

Allen MF, Crisafulli C, Friese CF, Jeakins SL (1992) Re-formation of mycorrhizal symbioses on Mount St Helens, 1980–1990 - interactions of rodents and mycorrhizal fungi. Mycol Res 96:447–453

Allen EB, Allen MF, Helm DJ, Trappe JM, Molina R, Rincon E (1995) Patterns and regulation of mycorrhizal plant and fungal diversity. Plant Soil 170:47–62

Amaranthus MP, Perry DA (1987) The effect of soil transfers on ectomycorrhizal formation and the survival and growth of conifer seedlings on old, nonreforested clearcuts. Can J For Res 17:944–950

Berch SM, Kendrick B (1982) Vesicular-arbuscular mycorrhizae of southern Ontario ferns and fern allies. Mycologia 74:769–776

Bergemann SE, Miller SL (2002) Size, distribution, and persistence of genets in local populations of the late-stage ectomycorrhizal basidiomycete, *Russula brevipes*. New Phytol 156:313–320

Borchers S, Perry DA (1987) Early successional hardwoods as refugia for ectomycorrhizal fungi in clearcut Douglas-fir forests of southwest Oregon. In: Sylvia DM, Hung LL, Graham JH (eds) Mycorrhizae in the next decade: practical applications and research priorities. University of Florida, Gainesville, pp 1–85

Brundrett MC (1991) Mycorrhizas in natural ecosystems. In: Macfayden A, Begon M, Fitter AH (eds) Advances in ecological research, vol 21. Academic, London, pp 171–313

Brundrett MC, Abbott LK (1994) Mycorrhizal fungus propagules in the jarrah forest. I. Seasonal study of inoculum levels. New Phytol 127: 539–546

Cooper KM (1976) A field survey of VA mycorrhizas in New Zealand ferns. N Z J Bot 14:169–181

Curran MP, Dunsworth BG (1988) Coastal red cedar regeneration: problems and potentials. In: Smith NJ (ed) Western red cedar-does it have a future? Conference proceedings, Faculty of Forestry, The University of British Columbia, Vancouver, BC pp 20–32

Daft MJ, El-giahmi AA (1978) Effect of defoliation and light on selected hosts. New Phytol 80:365–372

De Montigny L (1992) An investigation into the factors contributing to the growth check of conifer regeneration on northern Vancouver Island. Ph.D. Thesis, Department of Forest Sciences, University of British Columbia, Vancouver, BC

Ferguson JJ, Menge JA (1982) The influence of light intensity and artificially extended photoperiod upon infection and sporulation of *Glomus fasciculatus* on sudan grass and on root exudation of sudan grass. New Phytol 92:183–191

Fitter AH (1992) Roots. In: Davis B, Walker N, Ball D, Fitter A (eds) The soil. Harper Collins, London, pp 45–56

Francis R, Read DJ (1994) The contributions of mycorrhizal fungi to the determination of plant community structure. Plant Soil 159:11–25

Gehring CA (2003) Growth responses to arbuscular mycorrhizae by rain forest seedlings vary with light intensity and tree species. Plant Ecol 167:127–139

Gehring CA, Wolf JE, Theimer TC (2002) Terrestrial vertebrates promote arbuscular mycorrhizal fungal diversity and inoculum potential in a rain forest soil. Ecol Lett 5:540–548

Gemma JN, Koske RE, Flynn T (1992) Mycorrhizae in Hawaiian pteridophytes: occurrence and evolutionary significance. Am J Bot 79:843–852

Hagerman S, Sakakibara S, Durall, D (2001) The potential role for woody understorey plants to provide refuge for ectomycorrhizal inoculum at an interior Douglas-fir forest after clear- cut logging. Can J For Res 31:711–721

Hartnett DC, Wilson GW (1999) Mycorrhizae influence plant community structure and diversity in tallgrass prairie. Ecology 80:1187–1195

Hayman DS (1974) Plant growth responses to vesicular-arbuscular mycorrhiza. New Phytol 73:71–80

Hebda RJ (1983) Late glacial and postglacial vegetation history at Bear Cove Bog northeast Vancouver Island British Columbia Canada. Can J Bot 61:3172–3192

van der Heijden MGA, Boller T, Wiemken A, Sanders IR (1998a) Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79:2082–2091

Helgason T, Merryweather JW, Denison J, Wilson P, Young JPW, Fitter AH (2002) Selectivity and functional diversity in arbuscular mycorrhizas of co-occurring fungi and plants from a temperate deciduous woodland. J Ecol 90:371–384

van der Hiejden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998b) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72

Horton TR, Bruns TD (1998) Multiple-host fungi are the most frequent and abundant ectomycorrhizal types in a mixed stand of Douglas fir (*Pseudotsuga menziesii*) and bishop pine (*Pinus muricata*). New Phytol 139:331–339

Horton TR, Bruns TD, Parker VT (1999) Ectomycorrhizal fungi associated with *Arctostaphylos* contribute to *Pseduotsuga menziesii* establishment. Can J Bot 77:93–102

Husband R, Herre EA, Turner SL, Gallery R, Young JPW (2002) Molecular diversity of arbuscular mycorrhizal fungi and patterns of host association over time and space in a tropical forest. Mol Ecol 11:2669–2678

Jones MJ, Durall DM, Cairney JWG (2003) Ectomycorrhizal fungal communities in young forest stands regenerating after clearcut logging. New Phytol 157:399–422

Kleinbaum DG, Kupper LL (1978) Applied regression analysis and other multivariate methods, 1st edn. Duxbury, North Scituate, Mass., USA

Klironomos JN (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. Ecology 84:2292–2301

Kough J, Molina R, Linderman R (1985) Mycorrhizal responsiveness of *Thuja*, *Calocedrus*, *Sequoia* and *Sequoiadendron* species of western North America. Can J For Res 15:1049–1054

Kovacic DA, St. John TV, Dyer MI (1984) Lack of vesicular-arbuscular mycorrhizal inoculum in a ponderosa pine forest. Ecology 65:1755–1759

Kretzer AM, Dunham S, Molina R, Spatafora JW (2004) Microsatellite markers reveal the below ground distribution of genets in two species of *Rhizopogon* forming tuberculate ectomycorrhizas on Douglas fir. New Phytol 161:313–320

Lewis T (1982) Ecosystems of the Port McNeill block (block 4) of tree farm license 25. Internal report. Western Forest Products, Vancouver, BC

Lovelock CE, Andersen K, Morton JB (2003) Arbuscular mycorrhizal communities in tropical forests are affected by host tree species and environment. Oecologia 135:268–279

Miller SL, Allen EB (1992) Mycorrhizae, nutrient translocation, and interactions between plants. In: Allen MF (ed) Mycorrhizal functioning. Chapman & Hall, New York, USA, pp 301–332

Molina R, Massicotte H, Trappe JM (1992) Specificity phenomena in mycorrhizal symbiosis: community-ecological consequences and practical implications. In: Allen MF (ed) Mycorrhizal functioning. Chapman & Hall, New York, USA, pp 357–423

Moser M (1967) Die ectotrophe Ernährungsweise an der Waldgrenze. Mitt Forstl Bundesversuchsanst. Wien 75:357–380

Moyersoen B, Fitter AH, Alexander IJ (1998) Spatial distribution of ectomycorrhizas and arbuscular mycorrhizas in Korup National Park rain forest, Cameroon, in relation to edaphic parameters. New Phytol 139:311–320

Neter J, Kutner M, Nachtsheim C, Wasserman W (1996) Applied linear statistical models, 4th edn. Irwin, USA

O'Connor PJ, Smith SE, Smith FA (2002) Arbuscular mycorrhizas influence plant diversity and community structure in a semiarid herbland. New Phytol 154:209–218

Onguene NA, Kuyper TW (2002) Importance of the ectomycorrhizal network for seedling survival and ectomycorrhiza formation in rain forests of south Cameroon. Mycorrhiza 12:13–17

Overpeck JT, Bartlein PJ, Webb T (1991) Potential magnitude of future vegetation change in eastern North America-comparisons with the past. Science 254:692–695

Parent S, Messier C (1996) A simple and efficient method to estimate microsite light availability under a forest canopy. Can J For Res 26:151–154

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Perry DA, Amaranthus MP, Borchers JG, Borchers SL, Brainerd RE (1989) Bootstrapping in ecosystems. Bioscience 39:230–237

Prescott C, Weetman G (1994) Salal red cedar hemlock. Integrated research program: a synthesis. Faculty of forestry, The University of British Columbia, Vancouver, BC

Prescott CE, McDonald MA, Weetman GF (1993) Availability of N and P in the forest floors of adjacent stands of western red cedar-western hemlock and western hemlock-amabilis fir on northern Vancouver Island. Can J For Res 23:605–610

Read DJ (1991) Mycorrhizas in ecosystems. Experientia 47:376–391

Read DJ (1992) The mycorrhizal mycelium. In: Allen MF (ed) Mycorrhizal functioning. New Chapman & Hall, New York, USA, pp 102–133

Reynolds HL, Packer A, Bever JD, Clay K (2003) Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. Ecology 84:2281–2291

Sanders IR (2002) Specificity in the arbuscular mycorrhizal symbiosis. In: van der Heijden MGA, Sanders I (eds) Mycorrhizal ecology. Ecological studies analysis and synthesis, vol 157. Springer, Berlin Heidelberg New York, pp 415–440

SAS (1999) The SAS system for windows. Version 8.02. SAS Institute, Cary, N.C., USA

Terwilliger J, Pastor J (1999) Small mammals, ectomycorrhiza and conifer succession in beaver meadows. Oikos 85:83–94

Trappe JM (1989) The meaning of mycorrhizae to plant ecology. In: Mahadevan M, Ramen N, Natarayan K (eds) Mycorrhizae for green Asia. Centre for Advanced Studies. University of Madras, India, pp 347–349

Urcelay C, Diaz S (2003) The mycorrhizal dependence of subordinates determines the effects of arbuscular mycorrhizal fungi on plant diversity. Ecol Lett 6:388–391

Vandenkoornhuyse P, Ridgway KP, Watson IJ, Fitter AH, Young JPW (2003) Co-existing grass species have distinctive arbuscular mycorrhizal communities. Mol Ecol 12:3085–3095

Weber AB, Gilbert B, Kimmins JP, Prescott CE (2003) Factors limiting the early survivorship of *Thuja plicata* on northern Vancouver Island, British Columbia. Can J For Res 33:854–861

Zhi-wei Z (2000) The arbuscular mycorrhizas of pteridophytes in Yunnan, southwest China: evolutionary interpretations. Mycorrhiza 10:145–149