

Quantification of mycorrhizal limitation in beech spread

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Published on-line: 13 May 2012

Abstract: Establishment of *Nothofagus* spp. into grasslands can be limited by a lack of ectomycorrhizal inoculum, but the degree of mycorrhizal inoculum limitation and how far mycorrhizal inoculum spreads from forest edges has not been quantified. Further, it has been hypothesised, but not confirmed, that established *Kunzea ericoides* (a native Myrtaceae tree with both ectomycorrhizal and arbuscular mycorrhizal associations) could serve as an alternative host for ectomycorrhizal fungi and thus facilitate mycorrhizal infection of *Nothofagus*. To confirm and quantify these hypotheses, first we used an *ex situ*, intact-soil-core bioassay of soils collected near *Nothofagus solandri* var. *cliffortioides* forest, near established *Kunzea*, and in grassland distant from trees of either species. Second, we collected soils along transects of increasing distance from *Nothofagus* forest into adjacent grasslands. Mycorrhizal infection of *Nothofagus solandri* var. *cliffortioides* seedlings was high in soils from Near-*Nothofagus* and Near-*Kunzea* (74% and 67% of root tips, respectively) and lower in soils Distant from trees (28% of root tips). Seedlings in soils from Near-*Nothofagus* also had 3.4× greater biomass than those in soils Distant from trees. In the transects, mycorrhizal infection declined in a stepwise fashion at approximately 16 m distance from the forest edge, and seedling biomass was positively correlated with mycorrhizal infection. These data confirm that a lack of mycorrhizal inoculum can limit seedling establishment and show that *Kunzea* can provide an alternative host for *Nothofagus*-compatible mycorrhizal inoculum. Further, they provide quantitative data for spatially explicit models of woody establishment. Forty percent of seedlings in soils collected distant from trees had greater than 20% infection, suggesting that a lack of mycorrhizal inoculum is not a complete barrier to woody establishment, but instead may act as one of multiple environmental filters slowing beech spread.

Keywords: alternative hosts; facilitation; mycorrhizal inoculum; symbiosis; woody succession

Introduction

Nothofagus is a dominant or co-dominant tree genus in around 70% of New Zealand's indigenous forest area, yet shows limited regeneration into grasslands (Wardle 1984; Wiser et al. 2011). A lack of ectomycorrhizal inoculum more than 'one to two tree heights' from established trees was invoked by Baylis (1980) to explain the lack of *Nothofagus* spp. establishment into grasslands. This appears to have been the first report of mycorrhizal inoculum limitation of seedling establishment at a local scale. Since that seminal paper, a similar ectomycorrhizal-inoculum limitation has been reported for a wide range of other species, including various Pinaceae (Borchers & Perry 1990; Teste & Simard 2008; Collier & Bidartondo 2009; Nuñez et al. 2009), *Quercus* (Dickie et al. 2002), *Salix* and *Betula* (Nara & Hogetsu 2004). Further, seedlings establishing distant from trees have been found to be infected by a lower diversity of mycorrhizal fungi and distinct community of fungi when compared with seedlings establishing near trees (Deacon et al. 1983; Cline et al. 2005; Dickie & Reich 2005). Limitation by a lack of mycorrhizal inoculum has also been invoked as a possible explanation for the slow post-glacial spread of *Nothofagus* (Burrows & Russell 1990).

In contrast to the mycorrhizal limitation hypothesis, two studies have found that all *Nothofagus menziesii* seedlings greater than 10 cm in height had mycorrhizal infection, despite being distant from established trees (Allen 1987; Rogers 1989). In part these results may reflect the fact that only seedlings greater than 10 cm in height were measured

in both studies. Any seedlings without mycorrhizal infection would be unlikely to reach that height. Nonetheless, these findings suggest that *Nothofagus* spp. seedlings can sometimes establish in areas with limited inoculum. Once established, seedlings may then accumulate inoculum over time (Dickie et al. 2002). Similarly, 2-month-old *Nothofagus menziesii* seedlings in riverbeds lacked ectomycorrhizas yet were able to persist, while older individuals had mycorrhizas (Wardle 1980). A lack of mycorrhizal infection may therefore slow tree establishment, particularly in combination with other environmental filters such as competition, but cannot be taken as an absolute barrier to tree expansion (Dickie et al. 2007).

Further, *Leptospermum* or *Kunzea*, widespread native genera of Myrtaceae trees, could serve as alternative hosts for ectomycorrhizal fungi, and thereby facilitate *Nothofagus* establishment (Wardle 1980; Burrows & Russell 1990; Burrows & Lord 1993). *Leptospermum* and *Kunzea* are able to form symbioses with arbuscular-mycorrhizal fungi in addition to ectomycorrhizal fungi (Moyersoen & Fitter 1999; Weijtmans et al. 2007), which may permit them to establish into arbuscular-mycorrhizal grasslands and accumulate ectomycorrhizal-fungal inoculum over time. Facilitation of seedling mycorrhizal infection across plant species has been demonstrated in some other systems (e.g. *Arctostaphylos*–*Pseudotsuga* (Horton et al. 1999), *Helianthemum*–*Quercus* (Dickie et al. 2004), *Salix*–*Betula* and *Larix* (Nara 2006), *Arbutus*–*Quercus* (Richard et al. 2009)), but quantitative evidence is lacking for Wardle's proposed *Leptospermum*–*Nothofagus* interaction or any other Myrtaceae–Fagales interaction. Direct evidence is needed,

as many fungi have high levels of plant symbiont-preference (Tedersoo et al. 2008, 2010; Dickie et al. 2010), which might be expected to limit sharing of ectomycorrhizal fungi across lineages of ectomycorrhizal plants.

Thus, a number of key details remain unresolved more than 30 years after Baylis's first report of mycorrhizal limitation. Notably, (1) at what distance from trees is mycorrhizal inoculum limiting, (2) does mycorrhizal inoculum decline gradually or abruptly, and (3) do ectomycorrhizal *Kunzea* or *Leptospermum* provide an alternative host for fungi, and thus facilitate mycorrhizal infection of *Nothofagus* seedlings establishing in their vicinity? Understanding these details is critical to any attempt to integrate mycorrhizal limitation into more general models of forest establishment and spread, and carbon sequestration.

Methods

We used *ex situ* intact-soil-core bioassays to measure mycorrhizal inoculum in soils, as we did not believe it would be feasible to maintain first-year *Nothofagus* seedlings in the field. Intact soil cores introduce an unnatural element to the experimental design and may disrupt mycelial networks in soil. On the other hand, they have the advantage of isolating edaphic factors from above-ground effects of vegetation (Dickie et al. 2005) and correspond well with fungal communities observed in the field, provided disruption of soil is minimised (Avis & Charvat 2005).

We conducted two parallel experiments, with some replicates shared between the two experiments. Both experiments consisted of taking intact soil samples at different locations relative to a forest–grassland ecotone, or in proximity to established *Kunzea ericoides* within the grassland. The study site was river terrace grassland in the Korowai/Torlesse Tussocklands Park in mid-Canterbury that had been retired from grazing c. 50–60 years earlier (43°12.1' S 171°53.2' E, 560 m elevation). A mature *Nothofagus solandri* var. *cliffortioides* forest bordered the *Festuca novae-zelandiae* and *Agrostis capillaris* grassland on one edge, and *Kunzea ericoides* occurred as widely scattered individuals and clumps within the grassland. The site is described in more detail in Dickie et al. (2011), including detailed soil data from an adjacent, similar terrace. Other than *Kunzea ericoides* and *Nothofagus solandri*, no confirmed ectomycorrhizal host plants were present. There were, however, two species of Ericaceae (*Acrothamnus colensoi*, *Leucopogon fraseri*), present as very small individuals scattered throughout the grassland. There have been suggestions that some Ericaceae might support ectomycorrhizal fungi (Vrålstad et al. 2000; Villarreal-Ruiz et al. 2004) although this suggestion remains controversial (Vrålstad et al. 2002; Kohout et al. 2011).

Experiment 1 tested whether mycorrhizal infection of seedlings was higher in soils from near *Nothofagus* than in soils distant from *Nothofagus*, and determined how soils near *Kunzea* compared with these two treatments. We used 10 replicates of each of three treatments: Near-*Nothofagus*, Near-*Kunzea*, or Distant ($n = 30$). The Near-*Nothofagus* treatment was at the edge of *Nothofagus* forest, under the edge of canopy. The Near-*Kunzea* treatment was under the edge of a *Kunzea* canopy and at least 30 m from the nearest *Nothofagus*. The Distant treatment was at least 30 m from the nearest *Nothofagus* and at least 20 m from the nearest *Kunzea*.

Experiment 2 quantified the decline in mycorrhizal inoculum with distance from *Nothofagus*. We established five replicate transects with samples taken at 0, 4, 8, 12, 16, 20 and 30 m from the edge of *Nothofagus* canopy ($n = 35$). The 0-m and 30-m samples were included in Experiment 1 as Near-*Nothofagus* and Distant replicates, respectively ($n = 10$).

For both experiments, we obtained potted soil samples on 9 November 2010 by driving a metal coring device, lined with a 65-mm-diameter, 100-mm-long PVC pipe, into the soil, removing the top 1 cm with a sharp knife, and closing the bottom of the pipe with 1.5 mm nylon mesh, effectively potting the soil without disturbance. The coring device was scrubbed with a 50% bleach solution between samples. We bagged individual potted soil samples and transported these within 8 h to a 4°C storage room overnight before placing them on individual aluminium trays (to prevent water flow between pots) in a glasshouse and watering for 5 days.

Into each pot of soil ($n = 55$) we then planted a single *Nothofagus solandri* var. *cliffortioides* seedling that had been aseptically germinated in an autoclaved 50:50 vermiculite and peat moss substrate 60 days prior to potting. A 62% cover shade-cloth was placed over potted seedlings, and temperatures were maintained between 10°C and ambient. Seedlings were harvested after 190 days, on 23 May 2011. Prior experience had shown that shorter duration experiments resulted in difficulty in assessing mycorrhizal status (Dickie et al. 2002).

At harvest, we soaked seedling roots to loosen soil before washing them in flowing tap water. We examined all roots for ectomycorrhizal infection, counting all fine root tips, and recording whether each tip was ectomycorrhizal. For most seedlings, 50% of the root system was examined using a clear plastic grid and examining alternate rows under a stereo microscope (4× to 50×). On seedlings with fewer than 300 root tips, 100% of tips were examined (one seedling had 65 root tips; all others had more than 180 root tips). A subset of root tips were mounted on glass slides and examined with compound microscopy to confirm mycorrhizal assessments (presence of mantle, Hartig net, and/or extraradical hyphae; 40× to 1000×). Shoot (stem and leaves) and root tissues were separately dried, with shoot and root mass summed as seedling mass.

Statistical analysis

Seedling mass was log-transformed prior to analysis to account for the exponential nature of seedling growth. Ectomycorrhizal infection and growth in Experiment 1 was analysed as a simple factorial ANOVA ($n = 10 \times 3$ treatments), using Tukey's HSD for means separation among the three treatments. Data transformation was tested (arcsin square-root), but did not change results. We then used analysis of covariance (ANCOVA) to test for residual treatment effects on seedling growth after accounting for differences in ectomycorrhizal infection.

For Experiment 2, we used a three-parameter logistic model fitted with the *lme* function of R package *nlme*:

$$E = \alpha + \frac{\beta - \alpha}{1 + e^{(D-\lambda)}}$$

where E = ectomycorrhizal infection (0–100%), D = distance from forest edge (0 to 30 m), α = infection distant from trees, β = infection near trees, and λ is the distance at which mycorrhizal infection is halfway between α and β (Dickie & Reich 2005). The initial model was fitted with a random term for all parameters within a transect, with random terms removed through a process of iterative model simplification, selecting models that lowered

AIC values. The initial model was selected based on prior research (Dickie & Reich 2005; Dickie et al. 2005) and on the basis of having biologically reasonable properties.

Results

All seedlings survived for the duration of the experiments. Mycorrhizal infection (percentage of root tips) was highest in the Near-*Nothofagus* treatment and lowest in the Distant treatment ($P_{2,27} = 0.00072$), with the Near-*Kunzea* treatment not significantly lower in mycorrhizal infection than the Near-*Nothofagus* treatment (Table 1). In Experiment 1, seedling total dry weight was highest in the Near-*Nothofagus* treatment and lowest in the Distant treatment ($P_{2,27} = 0.021$), with the Near-*Kunzea* treatment intermediate and not significantly different from either (Table 1). Within Experiment 1, seedling total dry weight was strongly correlated with mycorrhizal infection (log-transformed mass; $P_{1,28} = 0.00036$, $R^2 = 0.35$). In ANCOVA, after accounting for the effect of mycorrhizal infection, there was no residual treatment effect on seedling dry mass.

In Experiment 2, mycorrhizal infection followed a step-wise logistic decline. An initial model fitted with random terms for each transect showed effectively no variation in mycorrhizal infection of seedlings near trees ($\beta = 72\%$) or in the distance from trees at which mycorrhizal infection declined ($\lambda = 15.91$ m), but mycorrhizal infection distant from trees was more variable (α , mean = 33%, range = 19–46%). Despite this variability, including a random term for a did not improve model fit compared with a model without that term.

Given the generally consistent model effects across transects, we combined data from Experiment 2 with the remaining Near-*Nothofagus* and Distant treatment data from Experiment 1 and fitted a model without a transect term (Fig. 1). The combined fit showed high mycorrhizal infection near trees ($\beta = 69\%$), declining at around 16.6 m (λ), to much lower levels distant from trees ($\alpha = 26\%$). Using all data from both experiments, seedling mass was positively correlated with mycorrhizal infection, although only slightly less than 20% of the variation in mass could be attributed to mycorrhizal infection (Fig. 2; $P_{1,53} = 0.0005$, $R^2 = 0.19$).

Discussion

A lack of ectomycorrhizal inoculum is likely to limit establishment of *Nothofagus* more than 16 m from the forest edge, but the presence of *Kunzea ericoides* can ameliorate this lack of inoculum. While the existence of mycorrhizal limitation

Table 1. Experiment 1: mycorrhizal and growth responses, showing mean (standard error). Values with different letters are significantly different at $P < 0.05$. Total seedling dry mass includes above- and below-ground (root) tissue.

Treatment	Ectomycorrhizal root tips (%)	Total seedling dry mass (mg)
Near- <i>Nothofagus</i>	74 (8) ^a	520 (140) ^a
Distant	28 (9) ^b	150 (35) ^b
Near- <i>Kunzea</i>	67 (6) ^a	280 (57) ^{a,b}

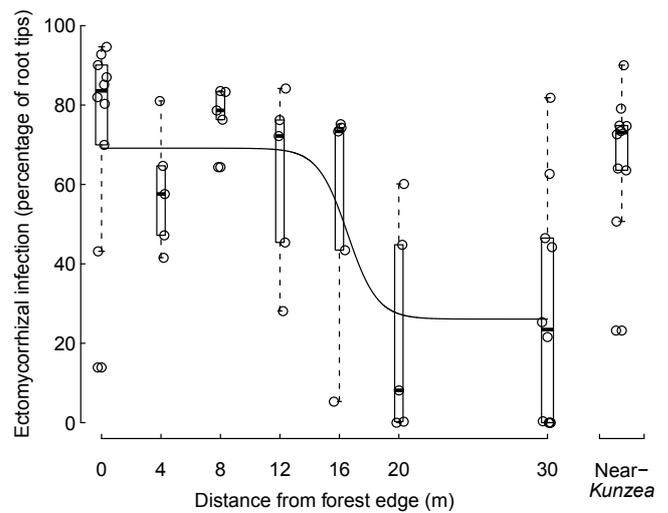


Figure 1. Seedling ectomycorrhizal infection (proportion of total root tips) as a function of distance from forest edge and for seedlings planted in soil near *Kunzea ericoides* and at least 30 m from the forest edge. Circles are individual seedling data points with a slight variance added to distance to avoid overlapping points. Line is a three-parameter logistic fit to the data. Boxes for each distance-group show 25th and 75th percentiles with median as solid horizontal line, and dashed lines indicating lesser of the range of data or 1.5 times the interquartile range. Box width is proportional to the number of observations in that group.

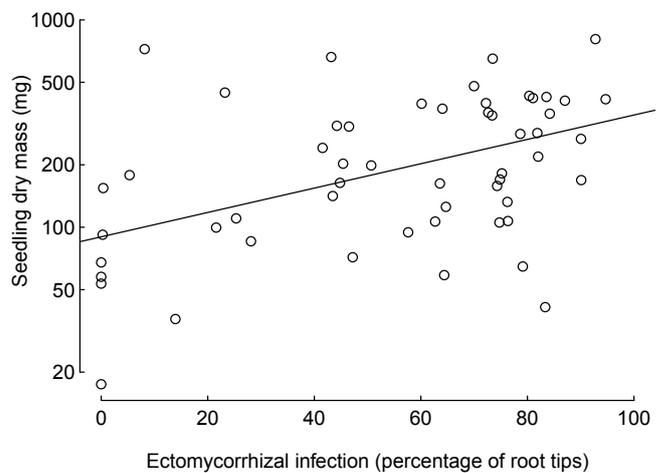


Figure 2. Seedling dry mass including both above- and below-ground tissue as a function of seedling ectomycorrhizal infection (proportion of total root tips), including data from both Experiment 1 and Experiment 2. Regression line is highly significant ($P_{1,53} = 0.0005$, $R^2 = 0.19$).

of *Nothofagus* was previously well known (Baylis 1980), these results provide the first quantification of mycorrhizal limitation of *Nothofagus* seedling establishment. Quantification is critical for incorporation of mycorrhizal limitation into ecosystem models examining multiple limitations on seedling establishment (Dickie et al. 2005, 2007) as well as more general understanding of the role of mycorrhizal limitation in the distribution of ectomycorrhizal trees (Leathwick 1998).

Cross-species facilitation of *Nothofagus* by *Kunzea* was suggested by Wardle (1980), but not previously

demonstrated. Tedersoo and colleagues (2008) suggested that late-successional *Nothofagus* may be particularly facilitated by sharing mycorrhizal partners with earlier successional Myrtaceae (*Eucalyptus* in that study), and our results support this hypothesis. At a broader scale, other plant species in the Fagales have been shown to benefit from shared mycorrhizal associations (Dickie et al. 2004; Richard et al. 2009), have a relatively low fungal-symbiont specificity (Tedersoo et al. 2008; Lang et al. 2011), and to facilitate the mycorrhizal infection of other species (Kennedy et al. 2003), although the order Fagales also includes *Alnus*, which has high symbiont specificity (Molina 1981).

Intriguingly, although mycorrhizal infection in the Near-*Kunzea* treatment was similar to that in the Near-*Nothofagus* treatment, seedling growth was only intermediate between the Near-*Nothofagus* and Distant treatments. This may reflect differences in the quality as opposed to the quantity of mycorrhizal inoculum, as the species of fungi associated with *Kunzea* may not be equally beneficial to *Nothofagus* as fungi associated with conspecific trees. Further studies should specifically address fungal community effects. Nonetheless, many other mechanisms are equally likely, including non-mycorrhizal effects of each plant species on soil nutrients. Greater understanding of mycorrhizal facilitation may allow the interaction to be used to facilitate rehabilitation of *Nothofagus* forest in environments where it has been removed by human activity (Weijtmans et al. 2007).

The relationship of mycorrhizal infection of *Nothofagus* with distance from the forest edge was similar to that previously described for *Quercus* (Dickie & Reich 2005). In both cases mycorrhizal infection of seedlings was high near established trees, declining rapidly at around 16 m from the forest edge to low levels distant from trees. This distance probably corresponds roughly to the lateral extent of the tree root systems (Stone & Kalisz 1991; Sudmeyer et al. 2004). While broadly similar in pattern, one key difference between the current study and prior work on *Quercus* was a higher level of mycorrhizal infection of seedlings distant from trees (33% compared with 8.6%). Other *in situ* studies have generally found very low levels of mycorrhizal infection of seedlings establishing distant from trees (Terwilliger & Pastor 1999; Collier & Bidartondo 2009; Nuñez et al. 2009). The current study was an *ex situ* bioassay. It is possible that a reduction in competition for both fungi and plants in potted soils permitted greater mycorrhizal infection even where inoculum levels were low. Any errors in handling would also have created a directional bias; potentially adding inoculum via cross contamination but unlikely to reduce it. Finally, the scattered presence of the small ericoid shrubs *Acrothamnus colensoi* and *Leucopogon fraseri* might have supported some ectomycorrhizal inoculum (Vrålstad et al. 2000; Villarreal-Ruiz et al. 2004) but further study is needed to determine if this actually occurs widely (Vrålstad et al. 2002; Kohout et al. 2011).

In Experiment 2, mycorrhizal infection and growth were both somewhat elevated at 0 m relative to all other distances. This may reflect better soil conditions, as under-canopy soils had noticeably higher organic matter than soils not under canopy (IAD, pers. obs., not quantified). We did not identify the species of fungi present on the roots of *Nothofagus* in this study, but Dickie and Reich (2005) found that soils under forest canopy had higher fungal diversity than soils only 4 m from the forest edge. An intriguing possibility is that the 0–4 m distance effects are driven by above-ground tree effects, including canopy interception of nutrients, which can

be elevated at forest edges (Weathers et al. 2001), and the input of leaf litter, which can strongly influence mycorrhizal communities (Dickie et al. 2009; Aponte et al. 2010). In contrast, the drop-off in mycorrhizal infection at 16 m is likely driven by the below-ground spread of tree roots. The logistic model we used in the present study does not adequately capture the elevated infection at 0 m.

The decline in mycorrhizal infection with distance from established trees is consistent with the restriction of seedling establishment to areas near forest margins (Wardle 1970; Wiser et al. 1997). Nonetheless, while our results support mycorrhizal inoculum as a factor limiting *Nothofagus* establishment into grasslands, they also illustrate that it cannot be the only factor limiting woody establishment. Adequate mycorrhizal infection extended 16 m from the forest, yet *Nothofagus* establishment even at the edges of grasslands is sporadic at best. Further, even in soils collected greater than 16 m from trees, about 40% of seedlings had greater than 20% mycorrhizal infection (Fig. 1).

We suggest that woody establishment into grasslands is limited by the additive and interactive effects of multiple barriers (Dickie et al. 2007). The combination of a lack of viable seeds, competition from exotic grasses, microclimate, herbivory, and a lack of mycorrhiza may prevent woody seedling establishment (e.g. Wardle 1970, 1984; Stevenson & Smale 2005), rather than any one factor in isolation. This pattern has been observed in other studies of old-field succession and may contribute to the difficulty in regenerating forest in post-agricultural successions (Cramer et al. 2008; Standish et al. 2009). The challenge for future research in this area will be characterisation of the multiple filters to woody invasion of grasslands and identification of cost-effective management interventions to overcome these barriers to woody regeneration.

Acknowledgements

N. Koele and M. St. John helped collect soils; R. Allen provided *Nothofagus* seed; K. Boot, G. Rattray and J. Thorn helped with planting, watering, root washing, weighing and data entry. This work is part of a larger collaboration that includes D. Peltzer and L. Burrows of Landcare Research, and N. Ledgard and T. Paul of Scion and is funded by the MAF – SLMACC (Sustainable Land Management and Climate Change) Fund (contract C04X1002 administered by the Ministry of Science and Innovation).

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Received 4 October 2011; 15 December 2011