Tree seedling performance and below-ground properties in stands of invasive and native tree species

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Abstract: The establishment and subsequent impacts of invasive plant species often involve interactions or feedbacks with the below-ground subsystem. We compared the performance of planted tree seedlings and soil communities in three ectomycorrhizal tree species at Craigieburn, Canterbury, New Zealand – two invasive species (*Pseudotsuga menziesii*, Douglas-fir; *Pinus contorta*, lodgepole pine) and one native (*Nothofagus solandri* var. *cliffortioides*, mountain beech) – in monodominant stands. We studied mechanisms likely to affect growth and survival, i.e. nutrient competition, facilitation of carbon and nutrient transfer through mycorrhizal networks, and modification of light and soil conditions by canopy trees. Seedlings were planted in plastic tubes filled with local soil, and placed in monospecific stands. Effects of root competition from trees and mycorrhizal connections on seedling performance were tested by root trenching and use of tubes with or without a fine mesh (20 μm), allowing mycorrhizal hyphae (but not roots) to pass through. Survival and growth were highest in stands of *Nothofagus* and lowest under *Pseudotsuga*. Surprisingly, root trenching and mesh treatments had no effect on seedling performance, indicating canopy tree species affected seedling performance through reduced light availability and altered soil conditions rather than below-ground suppression from root competition or mycorrhizal facilitation. Seedlings in *Pseudotsuga* stands had lower mycorrhizal colonisation, likely as a result of the lower light levels. Soil organic matter levels, microbial biomass, and abundance and diversity of microbe-consuming nematodes were all highest under *Nothofagus*, and nematode community assemblages differed strongly between native and non-native stand types. The negative effects of non-native trees on nematodes relative to *Nothofagus* are likely due to the lower availability of soil organic matter and microbial biomass in these stands, and therefore lower availability of resources for nematodes. This study shows that established stands of non-native invasive tree species may adversely affect tree seedlings and soil communities through modifications of the microenvironment both above and below ground. As such, invasion and domination of new landscapes by these species is likely to result in fundamental shifts in community- and ecosystem-level properties relative to those under native forest cover.

Keywords: invasive plants; mycorrhiza; nematodes; *Nothofagus solandri* var. *cliffortioides*; *Pinus contorta*; *Pseudotsuga menziesii*; root trenching

Introduction

Non-native, invasive plant species can have important effects on both the above-ground and below-ground components of terrestrial ecosystems, as well as on ecosystem functioning (Vitousek et al. 1987; Wolfe & Klironomos 2005; Van der Putten et al. 2007). While several studies have looked at the effects of invasive plants on both of these components (Ehrenfeld 2003; Wolfe & Klironomos 2005), the vast majority of these have considered plant invasion in herbaceous communities, and the impacts of invasive plants in forests is less well understood (Hughes & Uowolo 2006; Reinhart et al. 2006; Stinson et al. 2006). Further, much remains unknown about the mechanisms underlying the impacts of invasive species (Levine et al. 2003), particularly in forests (but see Stinson et al. 2006). As such, there have been few attempts to investigate the impacts of invasive species in New Zealand forests (but see Standish et al. 2004). This is despite there being a relatively large pool of naturalised introduced plant species in New Zealand, resulting in increased numbers of exotic species invading natural habitats (Williams & Cameron 2006).

Non-native tree species can have a range of effects both

above and below ground, and may influence establishing seedlings both positively and negatively. Negative effects include competition for resources, modification of the microenvironment, allelopathy, and apparent competition from herbivores or pathogens (e.g. Connell & Slatyer 1977; Tilman 1988; Cater & Chapin 2000). Positive effects (facilitation) may result from improvements of the physical environment by invasive trees, or the invasive species providing native plants with symbionts to improve resource uptake (Callaway 1995; Maestre et al. 2005). For example, mycorrhizal fungi may potentially play an important role in mediating the influence of invasive tree species on establishing tree seedlings. Mycorrhizal mutualisms may facilitate establishment of seedlings by increasing access to nutrients (Marschner & Dell 1994; Smith & Read 1997; Simard et al. 2002), or by transferring carbon (and nutrients) from already established plants through a common mycorrhizal network (Simard et al. 1997, 2002; Simard & Durall 2004). If native tree seedling species respond more positively than exotic species to native fungal species, this will act to promote the growth of native relative to exotic plant species (e.g. Dickie et al. 2002; Klironomos 2003). Conversely, if fungal species exert stronger positive effects on plant species that they are not usually associated with (Bever 2002), this may potentially promote invasion success. However, although tree seedlings may benefit from mycorrhizal connections with canopy trees, root competition from these trees may at the same time limit seedling growth and establishment (Coomes & Grubb 2000).

Invasive plant species can also exert important effects both above and below ground through influencing the decomposer subsystem. A handful of recent studies have focused on the effects of invasive plants on saprophytic microbial communities (Kourtev et al. 2002; Funk et al. 2005; reviewed by Wolfe & Klironomos 2005), although few have considered how invasive plants affect soil fauna involved in the decomposition process (Belnap & Phillips 2001; Yeates & Williams 2001; Belnap et al. 2005). Further, several recent studies have considered the impacts of invasive plants on decomposition (e.g. Ashton et al. 2005; Hughes & Uowolo 2006). Thus, invasive plants can often influence those soil organisms and processes that regulate the mineralisation of nutrients from plant litter and soil organic matter, and therefore the supply of nutrients from the soil for plant growth, including the growth of tree seedlings. However, the influence of invasive tree species on the decomposer subsystem has seldom been explored in forested ecosystems, including those in New Zealand (but see Yeates & Williams 2001; Standish et al. 2004).

Nothofagus solandri var. *cliffortioides* (mountain beech; hereafter *Nothofagus*) occurs in mountain areas throughout much of New Zealand, where it often forms monospecific stands with minimal if any ground layer vegetation (Wardle 1984). *Nothofagus* species, unlike most other New Zealand plant species, form ectomycorrhizal associations (Baylis 1980). Two of the most aggressively spreading non-native tree species in New Zealand, the North American conifers *Pinus contorta* (lodgepole pine; hereafter *Pinus*) and *Pseudotsuga menziesii* (Douglas-fir; hereafter *Pseudotsuga*), are widespread invaders in New Zealand, and are particularly abundant in mountain areas of of the South Island previously dominated by *Nothofagus* (Ledgard 2001). Like *Nothofagus*, these species are both ectomycorrhizal and have the capacity to form monospecific stands (Chu-Chou & Grace 1987; McKenzie et al. 2000). In this study, we examined impacts of established stands of invasive tree species (*Pseudotsuga* and *Pinus*), relative to stands of native species (*Nothofagus*), on seedling survival and growth of all three tree species, and on the key components of the decomposer subsystem (microbes and nematodes). Further, to investigate mechanisms influencing seedling establishment in native and non-native stands we used an experimental approach to study feedbacks between native and non-native trees and their seedlings resulting from changes in microclimate and resource availability, as well as the possible role of mycorrhizas and root competition in these feedbacks. By looking at impacts of the different stand types on both above- and below-ground properties, our intention was to better understand potential ecological effects of tree invasions relative to those of native forest vegetation, as well as the mechanistic basis underlying these effects.

Methods

Study area and tree species

The experiment was conducted in the Craigieburn Range, Canterbury, New Zealand, (43°58' S, 171°24' E, elevation 900–1100 m a.s.l), where *Nothofagus* is the only dominant native tree species. These forests were previously more extensive than their current distribution, before historical burning (Ledgard & Baker 1988; Wardle 1991). Introduced tree species were planted in this area in the 1950s to 1970s as part of trials to prevent erosion and for revegetation (Ledgard & Baker 1988), and now form adult stands. Similarly, many of these introduced species have spread from plantings for commercial purposes, farm shelterbelts and erosion control, and have subsequently become invasive in the Craigieburn Range and elsewhere in New Zealand (Ledgard 2001).

The two introduced North American conifers *Pinus* and *Pseudotsuga* were used to study ecological effects of invasive tree species. These tree species occur abundantly in the Craigieburn Range and were originally planted for erosion control or research trials. *Pinus* is widely distributed in its native range where it occurs from California (31°N) to the Yukon Territory (64°N), and is adapted to a range of soil types and climatic conditions

(Powers et al. 2005). *Pseudotsuga* occurs naturally from California (40°N) to Vancouver Island in British Columbia (51°N). The *Nothofagus* stands used in this study are natural stands interspersed among plantings.

Craigieburn has a mean annual temperature of 8.4°C, mean annual rainfall of 1559 mm, and mean annual solar radiation of 4458 MJ m^{-2} (1973–2002). The soils are Allophanic Brown Soils derived from greywacke, loess, and colluvium, with litter (L) and fermentation-humus (F-H) layers, an A-horizon of silt loam, and a stony B-horizon (Hewitt 1993). The soils are acidic, have high levels of exchangeable Al, and low base saturation (Matzner & Davis 1996).

Experimental set-up

Five replicate monospecific stands with fully developed canopies of each of the species *Nothofagus, Pseudotsuga* and *Pinus* were selected for use in the experiment. The 15 stands were (approximately) randomly distributed within the study area and the stands of the introduced species were positioned among stands of *Nothofagus*; all stands can therefore be considered as independent replicates. Stand characteristics are shown in Table 1. Two plots (2 × 2 m) were established in each stand, with one trenched and one left untrenched (control). The plots were trenched at the edges to a depth of 30–40 cm at three times during the course of the experiment.

The experiment involved seedlings planted into plastic tubes that were placed in the field (see Jones et al. 1989; Jones & Sharitz 1990), and was set up in a nested randomised design with four factors: stand type (*Nothofagus*, *Pseudotsuga* or *Pinus*), tree seedling species (*Nothofagus*, *Pseudotsuga* or *Pinus*), trenching treatment (trenched or untrenched plots), and mesh treatment (holes in tubes covered with mesh that only allows ingress by hyphae, or open holes that allow ingress by both roots and hyphae). Trenching treatments were nested within stand type, and tree seedling and mesh treatments were further nested within trenched and untrenched plots. The four combinations of trenching and mesh treatments enabled us to separate effects of root competition and mycorrhizal connections from adult trees. Three seedlings were used for each treatment combination in each of the five replicate stands used for each tree species. In total, the experiment consisted of 540 experimental units (i.e. tubes containing seedlings).

The tree seedlings used in the experiment were collected near the experimental stands. At the time of collection, the average seedling height and biomass was 54 mm and 74 mg for *Nothofagus*, 74 mm and 107 mg for *Pseudotsuga*, and 65 mm and 344 mg for *Pinus*. Seedling roots were cleaned of adhering soil and the seedlings were placed in vermiculite for 2–4 weeks prior to planting.

Soil was collected from each of the 15 stands and was homogenised, after removing litter, rocks and plant roots, to give 15 homogenous soils, each representative of the stand from which they were collected. The soil was then added to plastic PVC tubes (15 cm high, 5 cm in diameter). To prevent or allow root competition, the tubes each had eight holes (2 cm in diameter) that were either covered in 20-μm mesh (allowing mycorrhizal hyphae, but not roots, to pass through), or left open. For tubes with mesh, the mesh was also attached at the bottom to prevent roots from entering from below. For the remaining tubes, a coarser mesh (2 mm) was attached to the bottom of tubes and the holes were covered by decomposable paper to keep the added soil within the tubes prior to planting.

Seedlings were planted in the two types of tubes, with each tube containing soil collected from the experimental stand that they were to be placed into. The seedlings in tubes were positioned in the stands in May 2004 and were harvested in November 2005. To minimise soil disturbance and facilitate recolonisation by external mycelia, the tubes with seedlings were placed into form-fitting holes in the ground that were excavated with a soil corer, leaving 1–2 cm of the tube edge above the ground. They were placed in a grid at similar distances (20–30 cm) from each other.

We used local field-collected seedlings with low levels of mycorrhizal colonisation, rather than mycorrhizal-free seedlings grown from seed, mainly because the latter would be much less likely to establish and survive in our experimental plots after planting. We maintain that this should not exert a substantial effect on the outcome of the experiment, as the focus of the study was how mycorrhizal development and seedling growth subsequent to planting was affected by exclusion of roots and associations with mycorrhizae of canopy trees rather than seedling establishment per se, which may be more dependent on mycorrhizal colonisation.

Stand-level environmental characteristics

Several characteristics, e.g. microbial activity, light transmission, soil nutrient concentrations and pH, were measured for each of the 15 stands. Soil basal respiration and substrate-introduced respiration (SIR), which serve as relative measures of microbial activity and microbial biomass respectively, were determined on subsamples (10 g dry weight) of 4-mm sieved soil, following Wardle (1993). Briefly, the moisture content of the subsamples was adjusted to 150% by adding water or drying, and the soil subsample was then put in a 130-ml airtight bottle and incubated at 25°C for 24 h. For measurements of basal respiration, the CO_2 evolved in each container between 1 and 4 hours' incubation at 25°C was determined by injecting 1 ml of gas from the container headspace into an infrared gas analyser. Substrate induced respiration was determined the same way, as described by Anderson & Domsch (1978), but 0.2 g of glucose was added at the start of the incubation. Light radiation (photosynthetically active radiation – PAR) was measured for each stand and in nearby open areas (controls) on a clear day (1 × 80 cm integrated measure of PAR; four replicate measures;

AccuPAR ceptometer, Decagon Devices Inc., Pullman, Washington, USA). We measured PAR at similar times of the day for all plots, and always between 1100 and 1300 hours. Light transmission was calculated as the mean proportion of light reaching the sites relative to the controls. Soil organic matter content was determined as loss of ignition on dried samples (105°C, 12 h) that were ashed at 550°C for 2.5 h. The entire litter layer was collected in four circular subplots (diameter 35 cm) from each stand, dried at 60°C for 48 h and weighed. Root density (mass per unit soil weight) was measured at the end of the experiment in the trenched and untrenched plots, using five soil cores per plot (diameter 5 cm, depth 5 cm). Live roots were collected from the soil cores, dried at 60°C for 48 h and weighed. Soil pH was determined on a 1:2.5 mixture of soil and water. Total soil N and P were determined through the Kjeldahl method, plant-available P was quantified by measuring bicarbonate-extractable phosphorus, and nitrate and ammonium were determined colorimetrically on a Lachat flow injection analyser.

Harvest and measurements

At harvest, tubes were dug up and moved to a laboratory for examination. Soil subsamples were collected from each tube, and sieved to 4 mm for measurements of soil moisture content. Seedling heights were measured (ground level to apical bud) and roots were carefully washed clean under running water. To obtain a measure of root length and the total number of root tips in the root system, the entire root system was scanned and the resulting images analysed using WinRHIZO scanner and computer software (Régent Instruments Inc., Québec City, Canada). To assess effects of treatments on mycorrhizal colonisation of seedlings, we recorded presence or absence of mycorrhiza on 100 root tips on one seedling (out of the three planted) from each treatment combination in each replicate stand. The mycorrhizas were counted along line transects under a low-magnification microscope or on the whole root system if the seedling was small. Seedling root and shoot dry weight was measured after oven-drying (60°C, 48 h).

Soil subsamples for assessment of nematodes were taken from the vicinity of the seedling roots in those tubes harvested from untrenched plots, and were left unsieved. To assess impacts of stands of different tree species on soil nematodes, nematodes were extracted from a subsample (100 g wet weight) of soil from all tubes without mesh in untrenched plots, using a modified version of the tray method (Yeates 1978). The total numbers of nematodes in the samples were recorded by counting live specimens at 40× magnification. After fixing the suspension with an equal volume (to the soil) of boiling 8% formaldehyde, the nematodes were identified to nominal genus and allocated into six functional groups: bacterial feeders, fungal feeders, predators, omnivores, plant feeders, and plant associates.

Statistical analyses

Seedling variables were analysed using a mixed-model ANOVA testing for effects of stand type, trenching, mesh, and tree seedling species. As trenching treatments were nested within replicate stands, and randomly selected replicate stands were nested within stand type, site(stand type) and trench × site(stand type) were used as random factors in the model. All seedling response variables, except survival, were analysed as averages of all the surviving seedlings (up to three) planted in each experimental combination. When testing for changes in seedling growth, we analysed the absolute differences in biomass and height of seedlings at harvest and before the start of the experiment and used the initial seedling height as a covariate. For seedling biomass, the initial biomass was estimated by performing height–biomass regressions based on measurements of shoot height and dry biomass from 40 seedlings of each species, covering the whole size-range of the seedlings used in the experiment. Seedling survival was analysed using logistic regression.

Principal component analysis (PCA) was used to describe differences in nematode assemblage among treatments, and was performed on proportional data. The Shannon–Weiner diversity index was used as a relative measure of diversity of the nematode assemblage (Magurran 1988), and was determined as $H' = -\sum p_i \log_e p_i$, where p_i is the proportion of individuals in each taxon. Nematode abundance, diversity, and PCA scores were tested for the effects of stand type and tree seedling species using a mixed-model ANOVA, with replicate sites nested within stand type.

Seedling and nematode data were transformed when necessary to improve the normality and homogeneity of variances. The Tukey–Kramer test was used to evaluate differences between the least significant means following ANOVAS. Data analyses were performed using the procedure GLIMMIX (SAS Release 9.1, SAS Institute, 2002–2003) or SPSS 11.5.

Results

Site and soil characteristics

There were differences between stands of the different tree species for several of the measured site and soil characteristics (Table 1). Light transmission was greatest through stands of *Pinus* and least through stands of *Pseudotsuga*. Soil organic matter content and SIR were both significantly greater under *Nothofagus* than under *Pseudotsuga*. Meanwhile, stands of *Pseudotsuga* had the highest soil pH and, NO_3 and NH_4 concentrations. Soil moisture concentrations were significantly greater under stands of *Nothofagus* than under those of the other two species. Trenching resulted in a reduction of root biomass of 95%, 80% and 87% in stands of *Nothofagus*, *Pseudotsuga* and *Pinus*, respectively (Table 1).

Table 1. Site characteristics for stands of *Nothofagus, Pseudotsuga* and *Pinus*. Means and standard errors (in brackets) are shown. Within rows, numbers followed by different letters indicate significant differences at $P \leq 0.05$ (Tukey's test).

Site characteristics	*Nothofagus*	*Pseudotsuga*	*Pinus*
% light transmission	5.1 (1.5)*ab*	0.5 (0.1)*b*	13.3 (4.1)*a*
Soil basal respiration ($\mu g\ CO_2\ C\ g^{-1}\ h^{-1}$)	0.8 (0.3)*a*	0.5(0.2)*a*	0.5(0.3)*a*
Soil substrate-induced respiration ($\mu g\ CO_2\ C\ g^{-1}\ h^{-1}$)	9.3 (2.1)*a*	3.6 (1.1)*b*	4.6 (0.7)*ab*
Soil organic matter (%)	13.6 (0.01)*a*	9.8 (0.00)*b*	11.1 (0.01)*ab*
pH	4.8 (0.23)a	5.6 (0.14)*b*	4.9 (0.13)*ab*
$N0_3$-N ($\mu g\ g^{-1}$)	0.2 (0.09)*a*	4.6 (2.28)*b*	0.3 (0.07)*a*
NH_4-N ($\mu g\ g^{-1}$)	7.5 (2.4)*ab*	23.7 (8.6)*b*	4.7 (1.45)*a*
Total N (%)	0.38 (0.08)*a*	0.26 (0.03)*a*	0.32 (0.07)*a*
Olsen-P ($\mu g\ g^{-1}$)	18.1(2.5)*a*	17.5 (4.0)*a*	21.0 (3.9)*a*
Total P (%)	0.07 (0.01)*a*	0.07 (0.01)*a*	0.09 (0.01)*a*
Litter layer mass ($g\ m^{-2}$)	519.9 (100.5)*a*	634.6 (52.1)*a*	503.7 (68.1)*a*
Root density ($g\ dm^{-3}$):			
trenched plots	0.7 (0.06)*a*	0.3 (0.19)*a*	0.5 (0.27)*a*
untrenched plots	14.9 (3.22)*a*	1.5 (0.40)*b*	3.8 (1.82)*b*
Soil moisture (%):			
trenched plots	58.1 (2.4)*a*	41.8 (1.2)*b*	45.9 (1.1)*c*
untrenched plots	50.6 (1.6)*a*	39.6 (1.5)*b*	42.4 (1.6)*b*

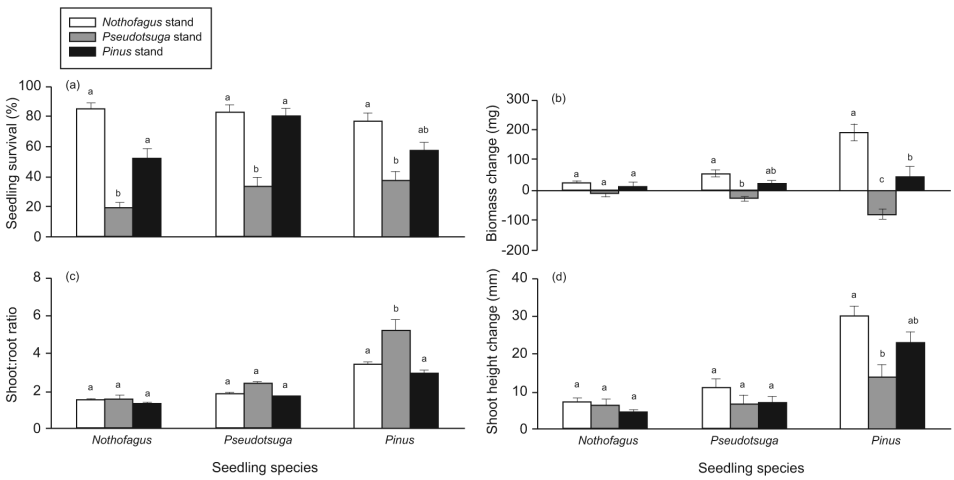

Figure 1. Survival and growth attributes (means + SE) of tree seedlings of *Nothofagus*, *Pseudotsuga* and *Pinus* in stands of the same three tree species: (a) survival, (b) biomass change (total biomass at harvest minus total initial biomass), (c) shoot: root ratio, and (d) shoot height change (shoot height at harvest minus initial shoot height). Different letters indicate significant differences between stands for each seedling species at $P \leq 0.05$ (Tukey–Kramer).

Tree seedling survival, growth, and mycorrhizal colonisation

The survival and growth of tree seedlings differed considerably among stand types (Table 2). Survival did not differ among seedling species; 58% of all seedlings survived the experimental period. However, survival was significantly higher in stands of *Nothofagus* and *Pinus* than in stands of *Pseudotsuga* (Fig. 1a). Seedling properties were largely unaffected by trenching and mesh treatments, with the exception of a slightly higher mycorrhizal colonisation in trenched plots (mean ± SE = 92 ± 1%) than in untrenched plots (89% ± 2%) (Table 2). The increase in total biomass of seedlings of all species at harvest relative to that at time of planting was three-fold higher in *Nothofagus* stands than in *Pinus* stands; in *Pseudotsuga* stands, the mean change in total biomass

Table 2. Effects of stand type, trenching, mesh, and tree seedling species on seedling growth attributes and mycorrhizal colonisation, as shown by *F*-statistics (*P*-values within brackets) from ANOVA and logistic regression for seedling survival[1]. Significant *P*-values are indicated in bold.

Seedling response variable	Stand type $F_{2, 12}$	Trenching $F_{1, 12}$	Mesh[2] $F_{1, 103}$	Seedling[2] $F_{2, 103}$	Stand* Seedling[2] $F_{4, 103}$
Seedling survival	25.07 (**<0.001**)	1.14 (0.307)	0.60 (0.441)	0.55 (0.577)	2.34 (0.058)
Change in seedling biomass[3]	14.41 (**<0.001**)	0.65 (0.436)	0.09 (0.762)	5.65 (**0.005**)	13.41 (**<0.001**)
Shoot: root ratio[4]	9.28 (**0.003**)	0.37 (0.555)	0.17 (0.680)	130.50 (**<0.001**)	5.46 (**<0.001**)
Shoot height change[3]	4.28 (**0.040**)	0.01 (0.936)	0.23 (0.632)	48.01 (**<0.001**)	3.02 (**0.021**)
Total root length	16.65 (**<0.001**)	0.08 (0.780)	0.06 (0.808)	39.22 (**<0.001**)	2.56 (**0.043**)
Root tip density (per unit root length)	11.34 (**0.002**)	0.03 (0.859)	0.10 (0.748)	282.62 (**<0.001**)	1.86 (0.123)
Mycorrhizal root tips (percent of total tips)[4]	22.64 (**<0.001**)	6.12 (**0.029**)	1.36 (0.247)	2.86 (0.062)	0.51 (0.731)

[1]Results are not presented for all two-way and three-way interactions as these were never statistically significant.
[2]Error d.f. for seedling survival = 135.
[3]Change refers to measurements at harvest minus measurements before planting.
[4]Data arcsine square root transformed.

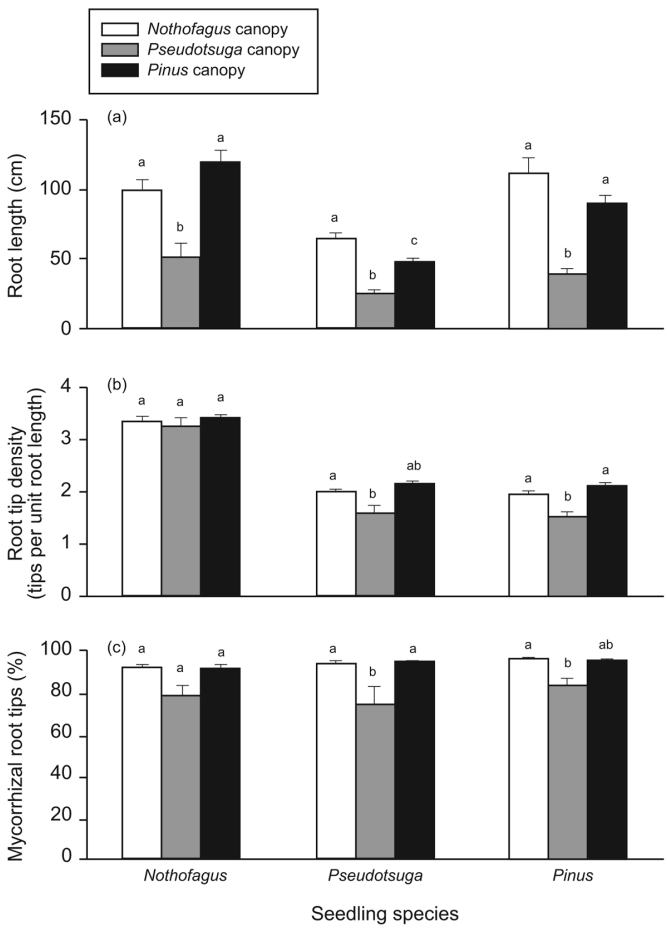

Figure 2. Root length, root tip density and mycorrhizal colonisation (means + SE) of tree seedlings of *Nothofagus*, *Pseudotsuga* and *Pinus* in stands of the same tree species: (a) root length, (b) root tip density, and (c) mycorrhizal root tips (percentage of total number of root tips). Legend as for Fig. 1.

was negative for all seedling species (Table 2, Fig. 1b). *Pinus* seedlings responded most strongly to stand type among seedling species, and had a very high biomass increase in *Nothofagus* stands. The net allocation of biomass to shoots and roots did not differ between stand types for *Nothofagus* and *Pseudotsuga* seedlings (Fig. 1c). *Pinus* seedlings had 67% higher shoot:root ratios in *Pseudotsuga* stands than in the other stands. Seedlings generally grew 70% taller under canopies of *Nothofagus* than under *Pseudotsuga*, and this was most pronounced for *Pinus* seedlings (Fig. 1d). Across species, seedlings had lower values for total root length, numbers of root tips per root length, and mycorrhizal colonisation of root tips in *Pseudotsuga* stands than in stands of the other species (Table 2, Fig. 2a–c). However, specific root length (i.e. root length / root mass) of seedlings did not differ significantly across the three stand types (data not presented). Mycorrhizal colonisation was generally high (80–100%) and did not differ significantly between seedling species (Fig. 2c).

Nematode abundance and community structure

Stand type had strong effects on nematode abundance, diversity, and community assemblage, but there were few effects of seedling species identity (Table 3). The total number of nematodes under *Nothofagus* was 14 times higher than under *Pseudotsuga* and 22 times higher than under *Pinus*. The abundances of bacterial feeding, fungal feeding and omnivorous nematodes were significantly higher in native stands than in stands of the introduced species, whereas the abundance of predatory nematodes did not differ significantly between stand types. There were no plant-feeding nematodes in the introduced stands and only 1.5 plant-feeding nematodes per gram of soil in the native stands (data not presented).

Nematode diversity was higher in *Nothofagus* stands than in the coniferous stands for all seedling species. There was also a small, but significant, effect of seedling species on nematode diversity; Shannon-Weiner diversity indices were significantly higher in tubes containing seedlings of *Nothofagus* (mean ± SE =1.62 ± 0.11) and *Pinus* (1.51 ± 0.17) than in tubes with *Pseudotsuga* seedlings (1.28 ± 0.18). The weak, but significant, stand type × seedling interactions for abundance of plant-associated and omnivorous nematodes, and nematode diversity, indicate that there was some variability in nematode abundance and diversity caused by tree seedling species identity. For example, tubes with *Nothofagus* seedlings had higher diversity than the coniferous seedlings in *Nothofagus* and *Pseudotsuga* stands, and *Nothofagus* and *Pinus* seedlings had higher diversity than *Pseudotsuga* in *Pinus* stands. Stand type had effects on ordination scores

Table 3. Effects of stand type and tree seedling species on abundances of nematode trophic groups and assemblages, shown by *F*-statistics (*P*-values within brackets) from ANOVA, and (in the case of stand type) data for nematode response variables (SEs in brackets). For the nematode responses to stand type, values within rows followed by the same letter are not statistically significant at $P \leq 0.05$ (Tukey–Kramer test). Significant treatment effects are indicated in bold.

Response variable	ANOVA results: treatment *F*, *P*			Data for nematode response to stand type		
	Stand type $F_{2, 11}$	Seedling $F_{2, 23}$	Stand * Seedling $F_{4, 23}$	*Nothofagus*	*Pseudotsuga*	*Pinus*
Total nematode abundance[1]	15.83 (**<0.001**)	1.87 (0.176)	1.89 (0.147)	4008.6 (1333.5)a	291.1 (77.3)b	184.4 (42.7)b
Bacterial-feeding nematode abundance[1]	14.27 (**<0.001**)	3.23 (0.058)	2.06 (0.119)	2232.6 (807.7)a	148.8 (62.2)b	62.5 (20.3)b
Fungal-feeding nematode abundance[1]	29.88 (**<0.001**)	1.13 (0.339)	0.45 (0.775)	890.0 (273.6)a	15.0 (7.9)b	9.9 (5.1)b
NCR[2]	4.68 (**0.034**)	1.59 (0.227)	0.73 (0.579)	0.63 (0.05)a	0.81 (0.13)ab	0.88 (0.06)b
Predatory nematode abundance[1]	0.20 (0.818)	0.33 (0.725)	1.78 (0.167)	403.6 (167.6)a	95.4 (25.8)a	77.0 (15.5)a
Plant-associated nematode abundance[1]	8.50 (**<0.001**)	1.60 (0.224)	3.41 (**0.025**)	190.9 (70.3)a	15.4 (10.5)a	15.0 (7.6)a
Omnivorous nematode abundance[1]	10.73 (**0.003**)	1.98 (0.161)	3.00 (**0.040**)	300.8 (92.9)a	16.5 (8.3)b	20.1 (5.3)b
Shannon-Weiner diversity index (H')	11.99 (**0.002**)	3.65 (**0.042**)	2.85 (**0.047**)	1.89 (0.05)a	1.08 (0.3)b	1.19 (0.1)b
PC1 (24%)[3]	4.25 (**0.043**)	1.77 (0.192)	2.26 (0.094)	0.37a	−0.79b	−0.06ab
PC2 (19%)[3]	7.03 (**0.011**)	0.47 (0.632)	0.05 (0.995)	0.79a	−0.40ab	−0.64b

[1]Number of nematodes g^{-1} soil dry weight. All ANOVAs done on log(X+1)-transformed data.
[2]Nematode Channel Ratio, i.e. the ratio of bacterial feeding to bacterial feeding + fungal feeding nematodes.
[3]Ordination axes derived from principal component analysis of the proportions of the main nematode genera in relation to the total nematode abundance in each pot. The percentage variance explained by each axis is within brackets. Ordination scores are rank-transformed.

for the two primary ordination axes (PC1 and PC2), and showed that the nematode community composition in *Nothofagus* stands differed from those of the introduced stands. Analysis of the nine most frequently found genera shows that native stands had a significantly lower percentage of predators (notably *Clarkus*) (F = 5.66, P = 0.020) and a higher percentage of fungal feeders (notably *Tylencholaimus*) (F = 26.42, P < 0.001) than the introduced stands (Fig. 3). There were no significant differences between stands for the other genera (data not shown). Further, NCR (i.e. the ratio of bacterial-feeding nematodes to bacterial- plus fungal-feeding nematodes) was higher in introduced stands compared with native stands (Table 3), although this was only significant for differences between *Nothofagus* and *Pinus* stands.

Discussion

Our results provide clear evidence of differences between adjacent stands that are dominated by three different tree species, one native and two non-native, with regard to their effects on both above-ground and below-ground properties. These measurements include the survival and growth of tree seedlings, and variables relating to organisms that influence decomposition such as soil microbial biomass and key groups of soil nematodes.

While our study provided evidence that performance of tree seedlings differed under stands of native and exotic tree species, we also sought to experimentally investigate the mechanistic basis of these effects. Despite showing that stand type influenced tree seedling survival and growth, root trenching and mesh treatments had no detectable effect on seedling performance. This is despite root trenching substantially reducing root biomass by >80% for all canopy tree species. This indicates that the differences in growing conditions between stand types, not effects of below-ground competition or supply of C and nutrients through mycorrhizal networks, was the main factor determining seedling growth and survival. Another possibility is that the planted seedlings had not reached sufficient size to deplete nutrients in their immediate vicinity (i.e. the tubes of root-free soil), and that effects of below-ground manipulations would only have become apparent once this nutrient pool was depleted or seedling roots had completely occupied available space within the experimental units (Grubb 1994). However, it is unlikely that this was important, given the relatively low concentrations of available mineral nutrients initially present in the bulk soil (Table 1).

Among the measured stand properties, light transmission and soil organic matter and moisture content differed most strongly between the stand types. The greater light transmission through the canopy of *Nothofagus*

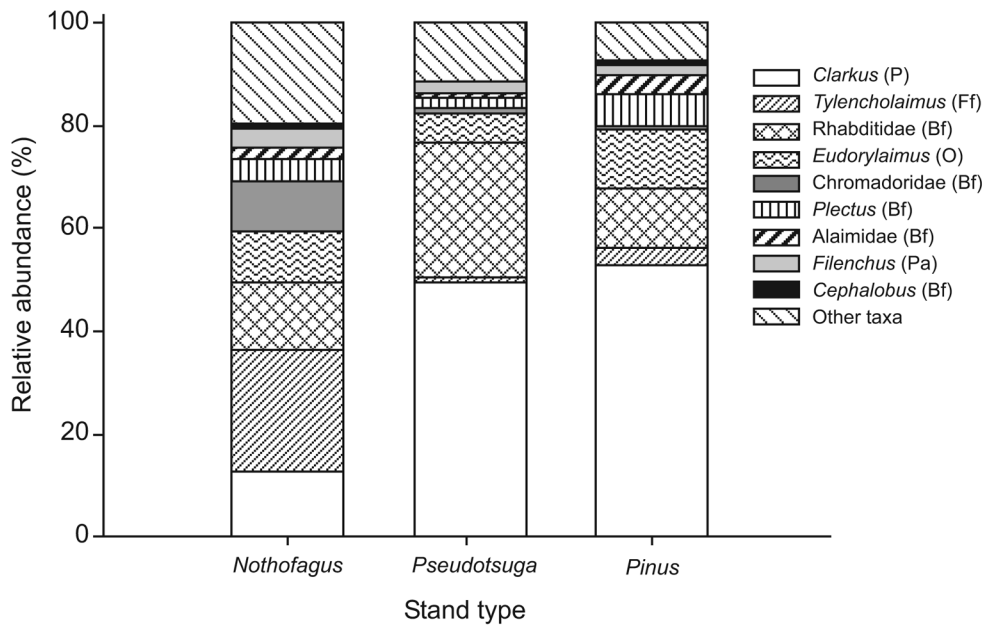

Figure 3. Relative abundance of the main nematode taxa in stands of *Nothofagus*, *Pseudotsuga* and *Pinus*. In the legend, the letters within brackets represent the functional group each taxon belongs to: P = predator, Ff = fungal feeder, Bf = bacterial feeder, and Pa = plant-associated.

relative to that of *Pseudotsuga* may partly explain why seedlings of both native and introduced species generally grew best in stands of *Nothofagus*. Light is a major factor for tree establishment, and tree growth has been shown to vary with gradients of light availability in forests (e.g. Lee et al. 1996; Claveau et al. 2002). Seedlings of all species had low survival rates and lost biomass under *Pseudotsuga* canopies where light transmission was very low. However, although *Nothofagus* stands provided the most favourable environment for the seedlings, the light levels in those stands were lower than in *Pinus* stands, indicating that other stand characteristics also had important impacts on seedling growth. Those factors are likely related to soil quality; soil organic matter, soil moisture, and densities of soil biota (active microbial biomass and nematodes) involved in nutrient mineralisation processes were all higher in *Nothofagus* stands than in the *Pinus* and *Pseudotsuga* stands (Table 1).

Tree species differ in their responses to light and nutrient availability (Latham 1992), and their level of shade tolerance has a major influence on their relative performance and long-term survival in shaded environments (e.g. Wright et al. 1998; Claveau et al. 2002). In our experiment, *Pinus* seedlings showed the strongest growth response to stand types among the seedling species, which may be explained by the relatively fast growth rate and low shade-tolerance of this species (Kayahara et al. 1996). In contrast, *Pseudotsuga*, which is known to be relatively shade tolerant (Bond et al. 1999), showed a much weaker growth response to stand type. *Nothofagus*, which probably has intermediate shade tolerance, also showed little growth response to stand type. Despite the marked difference among the three species in terms of shade tolerance, these three species were similarly unresponsive to trenching treatments; this is consistent with findings by Machado et al. (2003) who also found no differences in responsiveness to trenching of seedlings of tree species that differ greatly in shade tolerance. Shade intolerance has also been shown to promote shoot height growth in shaded environments (e.g. Aphalo et al. 1999), which may explain the high shoot heights of *Pinus* seedlings under both *Nothofagus* and *Pinus* canopies; under *Pseudotsuga* canopies the light conditions were probably too poor for the seedlings to grow significantly.

Nothofagus seedlings often occur on infertile soils under relatively closed canopies, where release from root competition through trenching may have the strongest effect on growth of seedlings (Coomes & Grubb 2000). In contrast to our study, Platt et al. (2004) found that trenching increased height and diameter growth of *Nothofagus* seedlings in stands of the same species, over a time frame comparable to that in our study. Although we found very large densities of roots in the upper soil layer in *Nothofagus* stands indicative of a very competitive environment for establishing seedlings (and a substantial reduction of root density following trenching), root trenching had no effect on planted seedlings. The *Nothofagus* seedlings used in the experiment of Platt et al. (2004) were naturally regenerated seedlings with greater (23–54%) shoot heights than those in our experiment, and these larger seedlings may have been able to better use nutrients created by the reduced root competition caused by trenching.

We predicted that survival and growth of seedlings would benefit from their connection to the mycorrhizal network formed by canopy trees, through influences on C and nutrient uptake of seedlings (Simard & Durall 2004). The seedlings in our experiment did not respond to either mesh or trenching treatments, again indicating that stand properties, rather than any associations involving root or mycorrhizal involvement, were most important in determining seedling establishment. In our study system, the mycorrhizal network should have been able to re-establish and connect with seedling root tips within weeks following insertion of tubes in the soil, given that the growth rate of the ectomycorrhizal mycelium can be 1 ± 4 mm per day under field conditions (Coutts & Nicoll 1990). However, any connections of this type that may have occurred were clearly unimportant in influencing seedling growth in our study.

The lower mycorrhizal root tip colonisation in *Pseudotsuga* stands than in stands of the other species is likely to be a consequence of the low light levels under canopies of this species. Several other studies have found mycorrhizal colonisation to be reduced in shaded environments (e.g. Ekwebelam & Reid 1983; Zhou & Sharik 1997; Gehring 2003). Low light availability has been associated with low photosynthetic rates, low root exudation, and low carbohydrate concentration in roots (e.g. Ferguson & Menge 1982; Smith & Read 1997), which are factors that are considered to be important for successful mycorrhizal colonisation (Smith & Read 1997). The poor seedling growth and low root tip density in *Pseudotsuga* stands suggest that the low mycorrhizal colonisation was a result of an overall loss in seedling vigour. Although mycorrhizal colonisation varied between the stand types, we found no interaction between seedling species and stand type on mycorrhizal colonisation. This is despite many ectomycorrhizal fungal species being host-specific, or having preferences for different tree species, which may limit the degree of mycorrhizal colonisation of seedlings under different canopy species (but see Dickie et al. 2006). However, our results may be due to the seedlings in our experiment already being colonised by mycorrhizas at the time of planting, and the colonisation of new root tips may have resulted from mycorrhizal fungi that had established before planting.

A growing number of recent studies have pointed to invasive plant species influencing the decomposer subsystem, and therefore potentially the decomposer processes that lead to the supply of plant-available nutrients from the soil (Ehrenfeld 2003; Wolfe & Klironomos 2005; Van der Putten et al. 2007). We found that invasive tree

species had a large negative effect on nematode abundance and in particular on those nematodes that directly consume saprophytic microbes. This is likely to be a consequence of lower levels of microbial biomass (i.e. food sources for the nematodes) in stands of the invasive species, as well as lower levels of soil carbon. Effects of invasive species were particularly adverse for the fungal-based (vs bacterial-based) energy channel of the soil food web, as the ratio of bacterial-feeding to fungal-feeding nematodes was greater under stands of the invaders. Importantly, these results point to invasive plant species strongly reducing densities of organisms known to be important in regulating plant-available nutrients; feeding by nematodes on microbial tissues is well known to release nutrients immobilised in microbes, thereby enhancing nutrient availability and plant growth (Ingham et al. 1985; Yeates 1987). It is therefore likely that the superior seedling growth under *Nothofagus* stands may be due in part to enhanced nutrient mobilisation caused by microbe-feeding nematodes and their consumption of soil microbial tissues.

The majority of studies on invasive plant impacts in natural ecosystems find that invaders promote decomposer organisms and processes relative to the native plants of the invaded community, largely because of improved quality of plant-derived resources returned to the soil (Ehrenfeld 2003; Allison & Vitousek 2004; Van der Putten et al. 2007). Our results are not consistent with this pattern. The reason why the invasive tree species support lower levels of decomposer biota than does *Nothofagus* is unclear, but may be a function of poorer quality of litter returned to the soil by the conifers (see Versveld & van Wilgen 1986), or reduced inputs of organic matter that maintain lower levels of decomposer organisms. This is consistent with other studies that have shown abundance of several trophic groupings in the soil food-web to be primarily regulated by resource availability (i.e. bottom-up controls) (e.g. Wardle & Yeates 1993; Mikola & Setälä 1998). In any case, our results serve as an example of potentially adverse effects of plant invasions for below-ground communities.

In combination, our results show that in areas previously covered by *Nothofagus,* the establishment of stands of the invasive tree species *Pseudotsuga* and *Pinus* can have very different effects from *Nothofagus* on a range of ecological properties both above and below ground. These include negative effects on seedling survival and growth and on components of the decomposer biota known to regulate ecosystem nutrient fluxes. There are significant areas of high country grassland in New Zealand (including in the vicinity of the study site), and elsewhere throughout the Southern Hemisphere, that were once under native vegetation but that are currently being rapidly invaded by introduced coniferous species (Richardson et al. 1994). Our results provide unambiguous evidence that established stands of invasive tree species may affect both tree seedlings and soil communities through modifications of the microenvironment, both above and below ground. As such, invasion and domination of new landscapes by coniferous species are likely to result in fundamental shifts in community- and ecosystem-level properties relative to native forest cover, and on both sides of the above-ground/below-ground interface.

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