# SHORT COMMUNICATION

# Mountain beech seedling responses to removal of below-ground competition and fertiliser addition

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**Abstract:** We examine the height growth, diameter growth and below-ground allocation responses of mountain beech (*Nothofagus solandri* var. *cliffortioides*) seedlings to the experimental removal of root competition through root trenching and the addition of fertiliser within relatively intact-canopied mountain beech forest in the Craigieburn Range, Canterbury. Trenching and trenching combined with fertiliser increased relative height and diameter growth of mountain beech seedlings above that of controls. Trenching and trenching combined with fertiliser also increased the root:shoot biomass ratio of seedlings above that of controls suggesting rapid root proliferation to maximise short-term nutrient uptake. Our results are consistent with an increasing number of studies that show that on infertile soils under intact canopies seedlings of 'apparent' light-demanding species can respond to the removal of root competition. Because New Zealand indigenous forests usually occur on infertile soils, we conclude that root competition may be particularly important.

**Keywords:** fertiliser; forest dynamics; New Zealand; *Nothofagus*; regeneration niche; root competition; seedling growth; seedling survival; trenching experiment.

## Introduction

A common view is that within a mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest understorey differences in light levels explain much of the variation in mountain beech seedling growth (see Cockayne, 1926; Wardle, 1984; Ogden *et al.*, 1996). This relationship, however, may not be causal since light levels and nutrient supply are both elevated in understoreys where the canopy is disturbed relative to those understoreys where the canopy is intact (e.g. Denslow *et al.,* 1990). There are two reasons why root competition for nutrients, rather than competition for light alone, could have a marked influence on seedling growth and mortality in mountain beech forest. Firstly, these forests have few plants in their understoreys (see Ogden *et al.*, 1996; Wiser *et al.*, 1998) despite a relatively large proportion of photosynthetically active radiation (PAR) penetrating to the forest floor (7.2% PAR transmission with a leaf area index of 7.8; John Hunt, Landcare Research, Lincoln, *unpubl. data*). Light transmission to the forest floor is high because the spatial and physical characteristics of mountain beech foliage result in a relatively uniform distribution of PAR through the canopy (Hollinger, 1989). Secondly,

it is expected that root competition will be greatest, with strong effects on nutrient availability, in infertile soils (e.g. Tilman, 1988; Grubb, 1994; Coomes and Grubb, 1998). We know mountain beech forest soils are relatively infertile (e.g. Allen *et al.*, 1997; Clinton *et al.*, 2002) and a fertiliser experiment confirmed that nitrogen is limiting to canopy tree productivity in these forests (Davis *et al.*, 2004). In this paper we examine growth responses by mountain beech seedlings to the experimental removal of root competition through root trenching and the addition of fertiliser under relatively intact mountain beech forest canopies.

## Materials and methods

Mountain beech is an evergreen tree species that lives up to 300 years, found between 36º and 46º S latitude, and which dominates comparatively dry montane and subalpine forests in eastern parts of New Zealand (Wardle, 1984). This study was conducted on the eastern slopes of the Craigieburn Range (43º15'S, 171º35'E, elevation 1050 m a.s.l.), Canterbury, where mountain beech extends from the valley bottoms at *c*. 650 elevation to treeline at 1400 m and is the only

canopy tree species (Wardle, 1984). This species is ectomycorrhizal and considered to be highly competitive on infertile soils (e.g. Wiser *et al.*, 1998). Like all New Zealand *Nothofagus,* mountain beech is shallow rooting with most lateral and fine roots concentrated in the upper 100–200 mm of soil (Wardle, 1991). Mountain beech seedlings occur on the forest floor under relatively intact canopies and in the absence of disturbance will survive in a quiescent state as advanced-growth seedlings for up to 30 years (Wardle, 1984).

At Craigieburn Forest Park climate station (914 m elevation), mean annual temperature is 8.0°C, mean annual precipitation 1447 mm and mean annual short-wave solar irradiance 4745 MJ/m$^2$ (McCracken, 1980). February has the maximum mean daily temperature (13.9°C) and July the minimum (2.0°C). Precipitation is well distributed throughout the year with only February, March and June having less than 100 mm each and trees are rarely subjected to moisture deficits (Benecke and Nordmeyer, 1982; Richardson *et al.*, submitted). Soils are predominantly Allophanic Brown Soils (Hewitt, 1993) derived from greywacke, loess and colluvium. They are steepland soils that have litter (L) and fermentation/humus (FH) layers over an A horizon of silt loam and a stony B horizon. Mineral soils in the study area have high amounts of exchangeable Al, extremely low base saturation, and are acidic (Davis, 1990; Matzner and Davis, 1996). Toppling of trees leads to small-scale pit and mound topography and results in within-stand variation in soil chemistry (Burns *et al.*, 1984; Allen *et al.*, 1997).

Our experimental site had a relatively intact mountain beech canopy with a uniform distribution of canopy trees and seedlings. On this site two 20-m tapes were laid out at right angles to each other and a distance along each was chosen using random numbers. These two distances formed the co-ordinates of one corner of a 1 × 1 m plot. A total of 40 plots were selected in this way using sampling without replacement and treatments were randomly assigned. The full design included controls, fertiliser, root trenching and a combination of fertiliser and root trenching as treatments. Each treatment was randomly applied to 10 replicate plots. Seedlings were thinned to a constant density of 10 seedlings (100–240 mm tall) per plot in November 1971. At that time the height and diameter (10 mm above ground level) of each seedling was measured and a spade used to carefully cut the tree roots around trenched plot perimeters to a depth of 250 mm. Fertiliser was applied in January 1972 as 20 g of calcium ammonium nitrate (equivalent to 200 kg/ha) and 50 g of serpentine superphosphate (equivalent to 500 kg/ha), with a maintenance application at the same rates in September 1972. The height, diameter and survival of seedlings in all plots were remeasured in April 1973

after two growing seasons (December to April; see Benecke and Nordmeyer, 1982). All live seedlings, without major shoot damage from falling branches, were carefully removed from the soil at this time with leaves, stems and roots of each seedling separated and their dry mass determined.

For each seedling we calculated relative growth rate in height ($R_H$) and diameter ($R_D$) using $R_X = (\ln(x_2) - \ln(x_1)/t$, where $x_1$ and $x_2$ were the initial and final measurements respectively and $t$ was the 1.42-year time interval between the two measurements (see Coomes and Grubb, 1998). Root:shoot biomass ratios were also calculated as a response variable for each seedling. Analysis of variance was used to compare treatment means for each response variable using PROC ANOVA in SAS for balanced designs (SAS Institute Inc., 1989). Comparisons among treatment means were made using Duncan's multiple-range test with the DUNCAN statement. Because differences in response variables among treatments may result from differential survivorship, we also used analysis of variance to test whether percent survival depended upon treatment.

# Results

Trenching and trenching combined with fertiliser increased mountain beech relative height growth, over two growing seasons, above that on controls (Fig. 1). The patterns of relative diameter growth among treatments were similar to those for relative height growth except that trenching combined with fertliser increased diameter growth above and beyond that of trenching alone and that trenching alone increased growth above that of fertiliser (Fig. 1). Overall, relative diameter growth was more responsive to the imposed treatments than relative height growth, and a combination of trenching and fertiliser gave a 231% increase in diameter growth above control seedlings, but height growth increased only 167% above controls. Trenching and trenching combined with fertiliser also increased the root:shoot biomass ratio of seedlings above that of controls (Fig. 1). Differences in each of the three response variables among treatments were not an artefact of differential survivorship as this was not significantly different among treatments (ANOVA $F = 1.46$, $P = 0.24$).

# Discussion

We observed a marked growth response by mountain beech seedlings to the removal of root competition under relatively intact-canopied forest over our two-growing-season experiment. That fertiliser addition
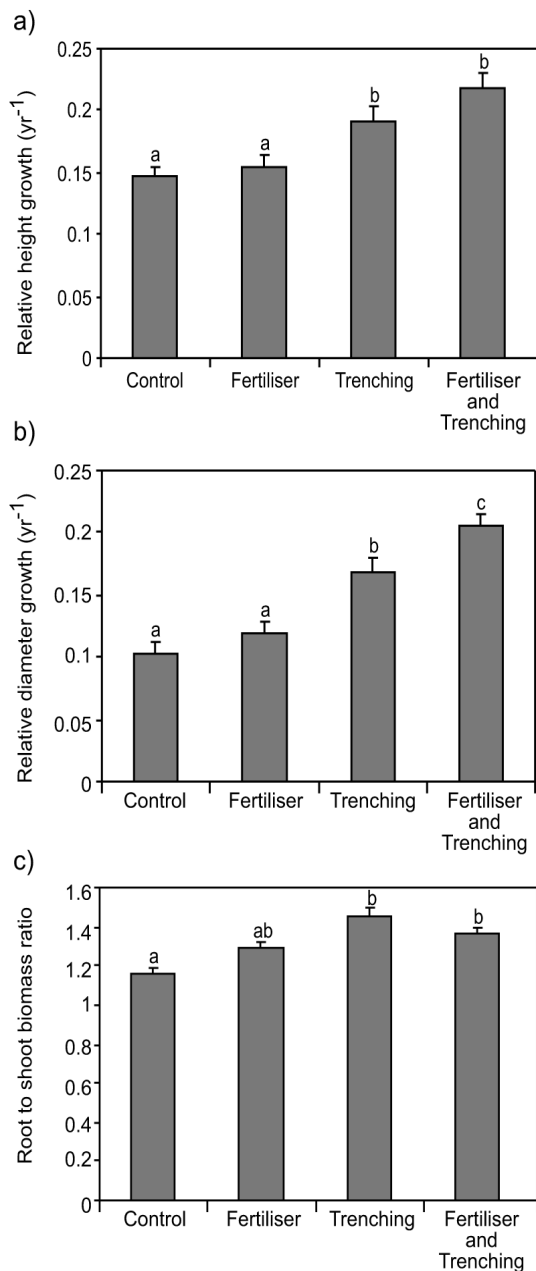
**Figure 1.** Mean relative growth rate in (a) height and (b) diameter of mountain beech seedlings over two growing seasons, as well as (c) final root:shoot biomass ratio, that were subjected to four treatments ($n = 10$). Error bars are ±1 standard error. Different letters show significant differences among treatment means ($P < 0.05$) using analysis of variance and Duncan's multiple-range test.

only increased seedling growth significantly when done in combination with trenching supports the view that enhanced seedling growth on these infertile soils only occurs when seedlings are protected from root competition with dominant trees (see Grubb, 1994; Coomes and Grubb, 2000). Structurally dominant trees may reduce soil nutrient availability to very low levels, and hence restrict seedling growth (Grubb, 1994; Coomes and Grubb, 2000). It has been suggested that decaying roots severed by trenching may act as an additional soil nutrient input (Berendse, 1983; Wardle, 1984) but other authors consider this unlikely to be of significance for seedling growth compared with the large effects of removing below-ground competition of neighbouring plants (e.g. McLellan *et al.,* 1995; Wilson and Tilman, 1995; Peltzer and Köchy, 2001). The increased below-ground allocation of seedlings when subjected to trenching or trenching combined with fertiliser may be a consequence of rapid root proliferation to maximise short-term nutrient uptake (Fig. 1; *cf.* Hutchings *et al.*, 2003) although an alternative expectation would be that seedlings would reduce below-ground allocation in response to fertiliser and trenching due to increased shoot growth (*cf.* Tilman, 1988; Lewis and Tanner, 2000). We conclude that our results are consistent with an increasing number of studies that show seedling performance of both 'apparent' light-demanding species (e.g. Cameron, 1960; Lewis and Tanner, 2000; Beckage and Clark, 2003) and shade-tolerant species (e.g. Putz and Canham, 1992; Lewis and Tanner, 2000) increases after removal of root competition on infertile soils under intact canopy forest.

Root competition has not previously been quantitatively demonstrated as a critical mechanism explaining regeneration patterns of a New Zealand *Nothofagus* species. Experimental manipulations and observations are now required to partition out the relative importance of above- (for light) versus below-ground (for soil resources) competition on seedling growth and survival along resource gradients. Lewis and Tanner (2000) showed that canopy gap creation (i.e. increased light and soil resources) explained 29% of deviance in seedling height growth in a Brazilian rainforest, whereas trenching (i.e. increased soil resources only) in the forest understorey explained 22% of the deviance. Similarly, Coomes and Grubb (1998) showed that trenching explained 44% of the deviance in seedling growth whereas gap creation explained only 6% of the deviance in a very infertile Amazonian caatinga forest understorey. We suggest that root competition is also a relatively important mechanism in beech forests, in part because canopy trees have well-developed ectomycorrhizae on shallow, dense root networks (see Wardle, 1984).

Root competition may be widely important in

New Zealand's indigenous forests because these forests usually occur on infertile soils (McLaren and Cameron, 1996; Pärtel, 2002). For example, Cameron (1960) has shown increased height growth by seedlings of two widely distributed New Zealand conifer tree species, *Dacrydium cupressinum* and *Podocarpus totara*, following trenching on infertile soils in the central North Island. In addition, nutrient limitation, rather than light, was the principal factor controlling photosynthesis by shade foliage in the understorey of *Dacrydium cupressinum* forest on an infertile soil in Westland, South Island (Whitehead *et al.,* 2004). Clearly there is a need for further systematic studies of how light, nutrients and competition, as well as their interactions, influence regeneration and species coexistence in the understorey of New Zealand forests.

## Acknowledgements

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