COMPARATIVE MINERAL NUTRITION OF *NOTHOFAGUS SOLANDRI* VAR. *CLIFFORTIOIDES* AND *N. MENZIESII* SEEDLINGS

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ABSTRACT

Nothofagus solandri var. *cliffortioides* (Hook.f.) Poole and *N. menziesii* (Hook.f.) Oerst. are both widely distributed in New Zealand, occurring naturally from sea level to the upper timberline. Despite the similarity in the distribution pattern between the two species, there are some areas where the natural stands of forests are either represented, or dominated by only one of the two species. To test the hypothesis that differences between *N. solandri* and *N. menziesii* in mineral nutrition may play a role in the localised distribution differentiation, we conducted two experiments examining the growth response of seedlings to the supply rates of five major nutrients, i.e., nitrogen, phosphorus, potassium, calcium, and magnesium, using the techniques of perlite and solution culture in a glasshouse. Results showed that *N. solandri* seedlings are less tolerant to supply limitations of phosphorus, magnesium, and calcium than are *N. menziesii* seedlings. These differences were related to the natural distribution of the two species.

Keywords: natural distribution; New Zealand; mineral nutrition; *Nothofagus menziesii*; *Nothofagus solandri*.

INTRODUCTION

The genetic divergence for more than 70 million years between the ancestral species of *Nothofagus solandri* var. *cliffortioides* (mountain beech) and *N. menziesii* (silver beech) has clearly differentiated physiological properties in relation to environmental conditions (Sun *et al.* 1995; Sun & Sweet 1996a, b). Differences have been found between *N. solandri* and *N. menziesii* seedlings in water relations and photosynthetic responses to light and temperature that might differentiate the two species in geographical distribution and ecosystem dynamics (Sun *et al.* 1995; Sun & Sweet 1996b). In addition to such factors as water relations (Sun *et al.* 1995) and the availability of seed source, edaphic factors may play a role in the spatial distribution of *Nothofagus* species in New Zealand, but this has not been well documented.

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Forest trees differ considerably in their capacity to absorb and utilise mineral nutrients, and in their tolerance to supply limitation of essential elements. Differences between plant species in nutrient requirements are important in relation to their adaptation to specific ecological habitats (Loneragan 1968). Species which are adapted to tolerate low rates of nutrient supplies are more likely to survive on sites of low fertility than plants requiring higher levels of nutrients; but they are often excluded from nutrient-rich sites because of their relatively slow growth. Knowledge of nutrient requirements is essential in the evaluation of the role of soil fertility in the biogeography of plants, and in the development of management strategies for the conservation of indigenous forest resources.

Detailed information on nutrient requirements of New Zealand *Nothofagus* species is lacking. From a study of foliar nutrient concentrations, Adams (1976) suggested that the species' distribution could be broadly related to soil fertility, but interpretation of results from foliar analysis of naturally grown stands can be difficult because of uncontrolled site factors. To test the hypothesis that the different local distributions of *N. solandri* and *N. menziesii* were due partly to the difference between the two species in their nutrient requirements, we studied seedling growth and nutrient uptake in relation to the supply rates of several essential macro-nutrients, using the perlite and solution culture technique in a glasshouse.

MATERIALS AND METHODS

Seedling Culture and Growth Conditions

Seedlings were raised in a glasshouse from seeds collected from Eglinton Valley in Fiordland National Park, in the south-west of the South Island (lat. 45°06'S, long. 167°58'E, alt. 270 m a.s.l). They were transplanted into 1-litre pots containing perlite 2 weeks after germination. Three seedlings of the same species were planted in each pot. At the time of transplanting, roots of all seedlings were carefully inoculated with mycorrhizal fungi by soaking them in a homogenate made of evenly mixed mycorrhizal-infected roots of naturally grown *N. solandri* and *N. menziesii* trees (the inoculation was shown to be effective as all seedlings displayed well-developed mycorrhizal roots at harvest). Lids made of 5-mm PVC foam were placed on the pots to avoid algal growth and evaporative water loss. All pots were placed on benches in the glasshouse and supplied with Ingestad's (1971) complete nutrient solution with nitrogen at 1.78 m*M* before nutrient treatments were applied. The environmental conditions in the glasshouse during experiment have been described previously by Sun & Sweet (1996b). Briefly, the maximum irradiance (PAR, 400–700 nm) during the growth period was about 1000 μmol/m^2·s. The day-length was extended to 16 h by using 400-watt sodium lamps directly above the benches. Temperature was thermostatically controlled, with the daily maximum and minimum at 25° (day) and 15°C (night), respectively.

Experimental Design and Treatments

Experiment 1

The design of Experiment 1 was a 2 (species) × 3 (nitrogen supply rates) × 3 (phosphorus supply rates) factorial arrangement, with four replications. The concentrations of nitrogen were 1.78, 7.14, and 14.28 m*M*, and those of phosphorus were 0.16, 0.42, and 0.81 m*M*. The intermediate levels were based on the work of Ingestad (1971) who found them optimal for

Betula verrucosa Ehrh.; the other two levels represented deficient and excessive rates of supply. Other essential nutrients were maintained constant at the levels defined by Ingestad (1971) as optimum in relation to nitrogen at 7.14 m*M*. Treatments began 1 week after transplanting was carried out. Fresh nutrient solutions were fed to seedlings with a frequency increasing from once every 14 days in the first month to twice a week for the last 3months. At each application, 500 ml of solution were applied to each pot from the top, displacing the residual solution which was allowed to drain freely through holes at the base. At other times pots were placed on individual saucers as a pre-caution against contamination. They were arranged randomly on the same bench and re-arranged after each nutrient application. The treatments were continued for 6 months before seedlings were harvested for growth and nutrient analysis.

Experiment 2

The design of Experiment 2 was a 2 (species) × 2 (calcium supply rates) × 3 (potassium supply rates) × 3 (magnesium supply rates) factorial arrangement with four replications. The concentrations of calcium were 0.025 and 0.25 m*M*, those of potassium were 0.026, 0.26, and 2.6 m*M*, and those of magnesium were 0.004, 0.04, and 0.4 m*M*. All other nutrients were as in Ingestad's (1971) complete nutrient solution. Nutrient solutions were applied as described for Experiment 1. Experiment 2 was run for 15 weeks.

Biomass and Tissue Nutrient Analysis

Immediately after harvesting in each experiment, each seedling was divided into shoot and roots, and oven-dried at 70°C for 48 h to determine the dry weight of each subdivided component (i.e., shoot dry weight, DW_{Sh}, and root dry weight, DW_{Rt}) and the root to shoot ratio (RSR). In Experiment 1, oven-dried samples of shoots and roots from the same pot were bulked and analysed for concentrations of nitrogen (C_{N}) and phosphorus (C_{P}) after digestion using an auto-analyser (Nicholson 1984). The concentrations of calcium (C_{Ca}), potassium (C_{K}), and magnesium (C_{Mg}) of the oven-dried samples from Experiment 2 were analysed after digestion using an atomic absorption spectrophotometer. The uptake rates (U) of the nutrients per unit of root dry weight were calculated using the formula of Ingestad & Ågren (1988):

$$U = \frac{10^6\, C_i}{M}\,[e^{RGR} - 1]\,\frac{DW_T}{DW_{Rt}}$$

where C_i is the concentration of the nutrient in the seedling, M the molecular weight of the nutrient, e the base of natural logarithm, DW_T and DW_{Rt} the dry weight of the whole seedling and roots, and RGR the mean relative growth rate, which was calculated by:

$$RGR = \frac{\ln DW_T - \ln DW_0}{\Delta T}$$

where DW_0 is the seedling initial dry weight estimated by destructively sampling six seedlings of similar sizes, and ΔT is the duration of the experiment in hours.

Data Analysis

Data were evaluated by analysis of variance (ANOVA) for a completely randomised design in a factorial arrangement involving the factors concerned. The statistical analysis was performed with the ANOVA procedure of SAS® System for Windows™ release 6.12 (SAS Institute Inc. 1989).

RESULTS

Growth Response to Nitrogen and Phosphorus Supply

In both *N. solandri* and *N. menziesii*, DW_{Sh} and DW_{Rt} were highly significantly ($p < 0.0001$) affected by an interaction between the rates of nitrogen and phosphorus supply; both DW_{Sh} and DW_{Rt} were greatest in seedlings grown at 7.14 m*M*[N] and 0.81 m*M*[P], but decreased with any further change in nitrogen supply or decrease in phosphorus supply (Fig. 1). Increasing phosphorus supply had an adverse effect at 1.78 m*M*[N], but a positive effect at 7.14 m*M*[N], on both DW_{Sh} and DW_{Rt} in both species. At 14.28 m*M*[N], deficient phosphorus supply reduced both DW_{Sh} and DW_{Rt} in *N. solandri*, but had no effect in *N. menziesii*. When the rate of phosphorus supply was low, decreasing the rate of nitrogen supply decreased DW_{Sh} and DW_{Rt} in *N. menziesii* mainly from 7.14 to 1.78 m*M*[N], but increased DW_{Rt} from 14.28 to 1.78 m*M*[N] and had no effect on DW_{Sh} in *N. solandri* (Fig. 1).

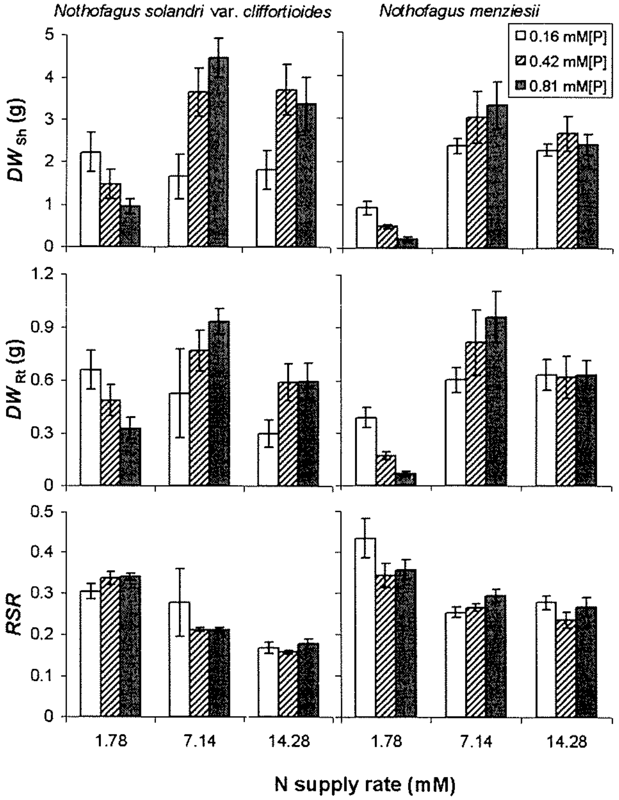

FIG. 1–Dry weights of shoots (DW_{Sh}) and roots (DW_{Rt}), and root to shoot ratio (*RSR*), in 6-month-old *N. solandri* and *N. menziesii* seedlings grown at different rates of nitrogen and phosphorus supply in perlite and solution culture. Vertical bars indicate 2× standard error (n = 4)

Nothofagus solandri seedlings had greater DW_{Sh} than *N. menziesii* seedlings under all conditions except under adequate or excessive nitrogen supply but limited phosphorus supply.

RSR was significantly ($p < 0.0001$) reduced with increasing nitrogen supply, and was, with one exception (7.14 m*M*[N] and 0.16 m*M*[P]), 25% greater in *N. menziesii* than *N. solandri* (Fig. 1).

Concentrations and Uptake Rate of Nitrogen and Phosphorus

C_N was affected significantly by the rate of nitrogen supply ($p < 0.0001$), and by an interaction between species and the rates of nitrogen and phosphorus applied ($p < 0.01$). The interactive effect between the rates of nitrogen and phosphorus supply on C_N was highly significant ($p < 0.0001$) in *N. solandri*; C_N increased with increasing rates of nitrogen supply, with the response adversely affected by increasing phosphorus supply at the higher rates of nitrogen (Fig. 2). In *N. menziesii*, C_N responded highly significantly ($p < 0.0001$) to the rate of nitrogen without the interference of phosphorus supply.

U_N increased highly significantly ($p < 0.0001$) with increasing rates of nitrogen (Fig. 2). The response of U_N to the rate of nitrogen supplied differed significantly ($p = 0.0001$) between *N. solandri* and *N. menziesii*. Although the values of U_N were nearly the same for the two species at 1.78 m*M*[N], with increase in the rate of nitrogen supply *N. solandri* showed a much greater increase in U_N than *N. menziesii*.

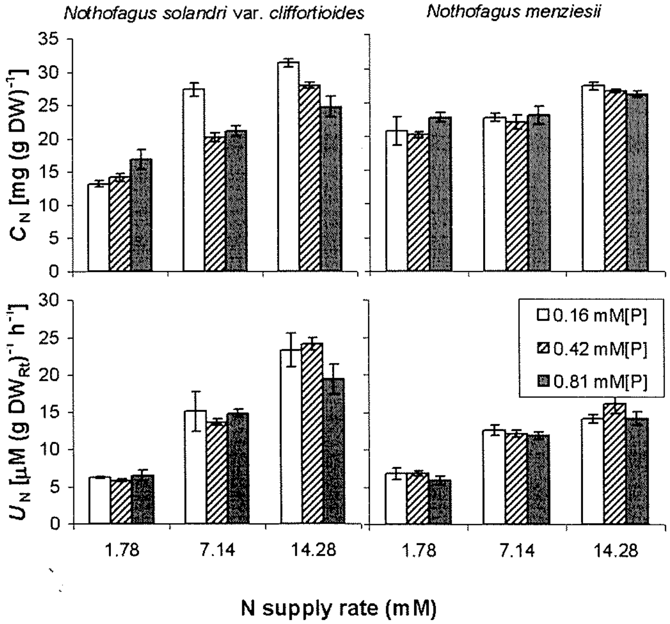

FIG. 2–Tissue nitrogen concentration (C_N) and uptake rate (U_N) in 6-month-old *N. solandri* and *N. menziesii* seedlings grown at different rates of nitrogen and phosphorus supply in perlite and solution culture. Vertical bars indicate 2× standard error (n = 4)

Both C_P and U_P were predominantly and positively related to the rate of phosphorus supply (Fig. 3). The values of C_P in *N. menziesii* were greater than in *N. solandri* across nearly all the treatments. On average, C_P was 58% greater in *N. menziesii* than in *N. solandri*. U_P responded positively to the rate of phosphorus supply in all except the high rate of phosphorus at the lowest rate of nitrogen.

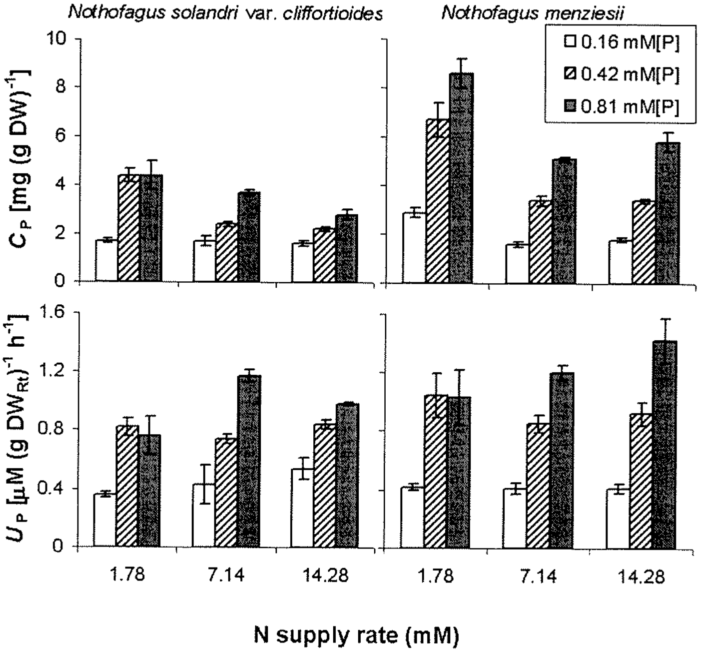

FIG. 3–Tissue phosphorus concentration (C_P) and uptake rate (U_P) in 6-month-old *N. solandri* and *N. menziesii* seedlings grown at different rates of nitrogen and phosphorus supply in perlite and solution culture. Vertical bars indicate 2× standard error (n = 4)

Growth Response to Calcium, Potassium, and Magnesium Supply

Among the three nutrients investigated, magnesium appeared to affect the seedling growth most in both species. Both DW_{Sh} and DW_{Rt} decreased significantly ($p < 0.0001$) with decreasing magnesium supply (Fig. 4). Severe chlorosis was displayed in seedlings grown at 0.004 m*M*[Mg] (data not shown). The chlorosis occurred in older leaves first, and moved gradually into younger leaves. At the lowest rate of magnesium, *N. menziesii* seedlings had significantly ($p < 0.05$) greater DW_{Sh} and DW_{Rt} than *N. solandri* seedlings.

A decrease in calcium supply rate from 0.25 to 0.025 m*M* significantly ($p < 0.05$) reduced DW_{Sh} in *N. solandri*, but did not affect the growth of *N. menziesii* (Fig. 4). Changes in the potassium supply rate did not have a significant effect on DW_{Sh} or DW_{Rt} in either species.

In *N. solandri*, *RSR* was significantly ($p < 0.001$) reduced by increasing magnesium supply rate and increased by increasing potassium supply rate in treatment with calcium at 0.025 m*M*; whereas in *N. menziesii*, *RSR* was affected by none of the nutrients.

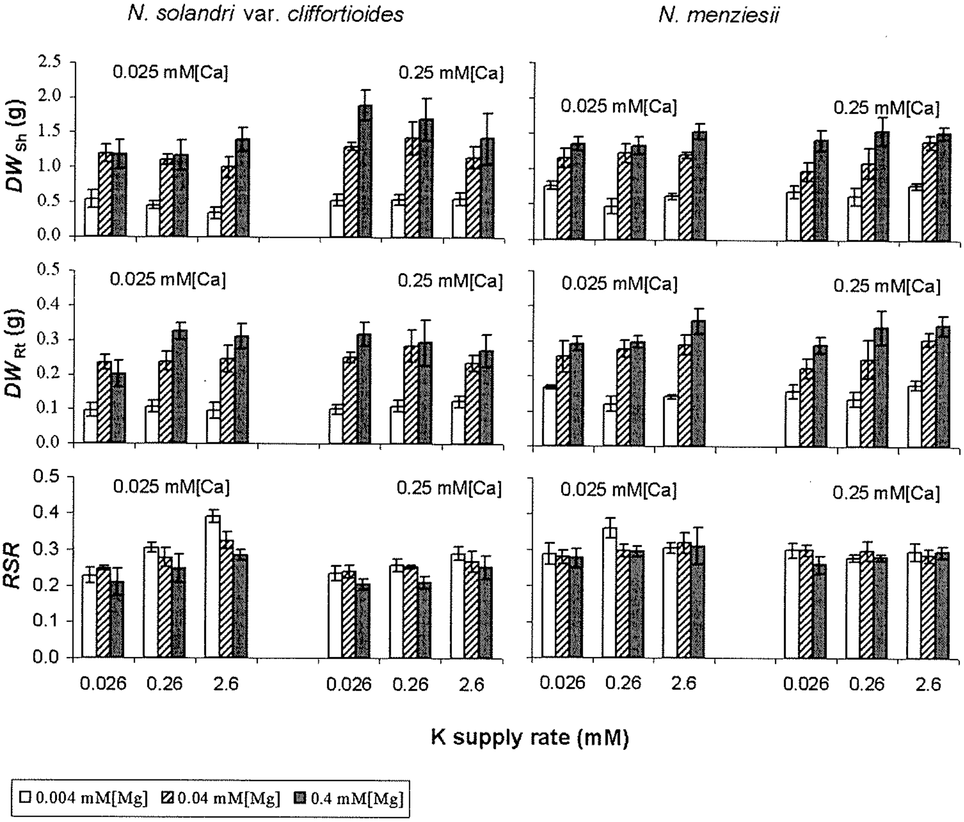

FIG. 4—Dry weights of shoots (DW_{Sh}) and roots (DW_{Rt}), and root to shoot ratio (*RSR*), in 15-week-old *N. solandri* and *N. menziesii* seedlings grown at different rates of calcium, magnesium, and potassium supply in perlite and solution culture. Vertical bars indicate 2× standard error (n = 4)

Concentrations and Uptake Rate of Potassium, Magnesium, and Calcium

Both C_K and U_K decreased significantly ($p < 0.0001$) with decreasing potassium supply rate, but increased with decreasing magnesium supply rate (Fig. 5). In *N. solandri*, C_K was significantly ($p < 0.001$) greater in seedlings grown at 0.025 than at 0.25 m*M*[Ca]. The two species did not differ in C_K and U_K, regardless of the treatments.

C_{Mg} and U_{Mg} decreased significantly ($p < 0.0001$) with decreasing magnesium supply rate, but increased with decreasing potassium supply rate when grown at 0.4 m*M*[Mg] (Fig. 6). *Nothofagus solandri* was significantly ($p < 0.0001$) more responsive to changes in magnesium supply rate than *N. menziesii*. In *N. solandri*, the response of C_{Mg} to changes in magnesium supply rate was slightly ameliorated ($p < 0.01$) by a high rate of calcium supply.

C_{Ca} and U_{Ca} decreased significantly ($p < 0.0001$) with decreasing calcium supply rate, but increased with decreasing magnesium supply rate (Fig. 7). The effect of calcium supply rate on both C_{Ca} and U_{Ca} was much more pronounced in *N. solandri* than in *N. menziesii*.

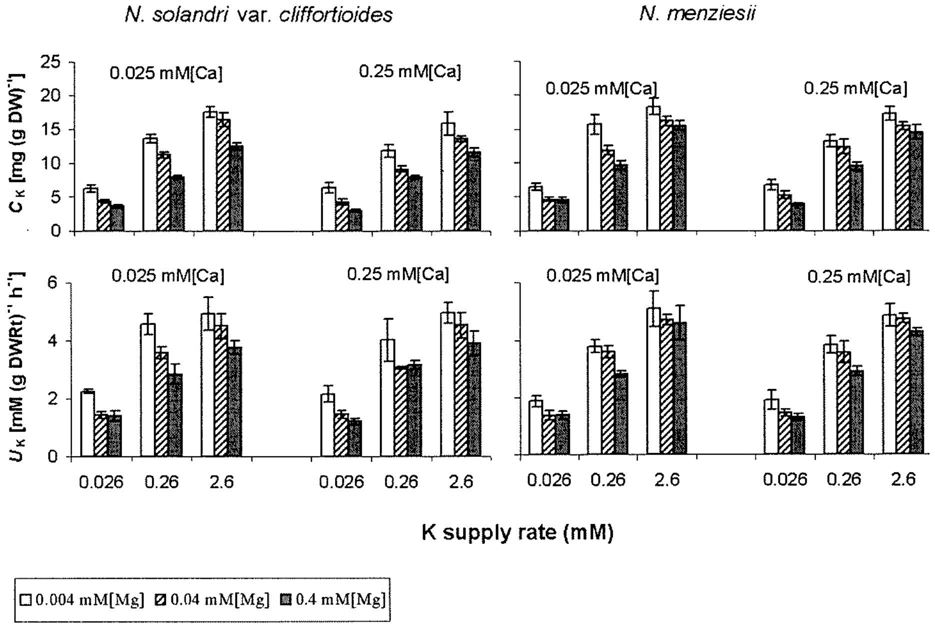

FIG. 5–Tissue potassium concentration (C_K) and uptake rate (U_K) in 15-week-old *N. solandri* and *N. menziesii* seedlings grown at different rates of calcium, magnesium, and potassium supply in perlite and solution culture. Vertical bars indicate 2× standard error (n = 4)

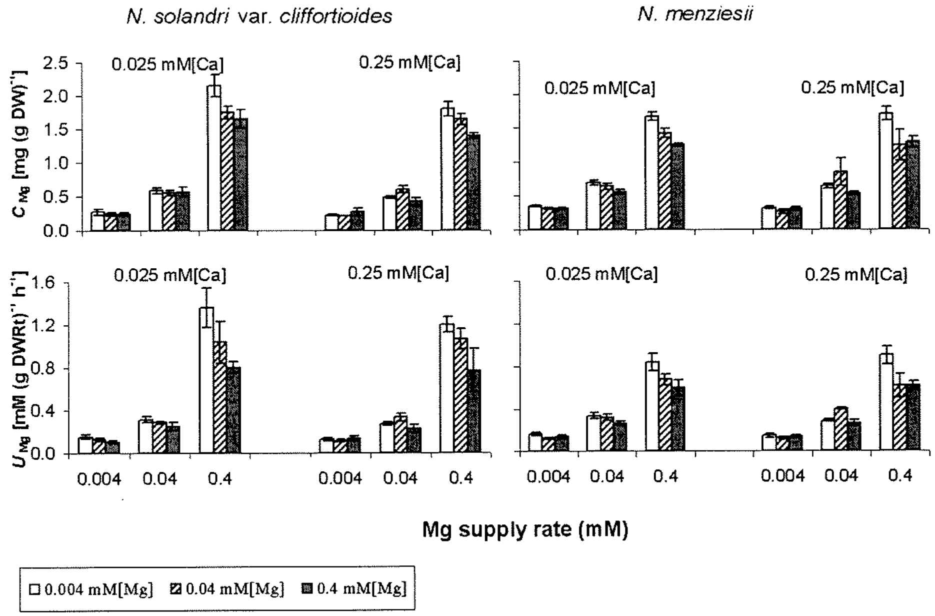

FIG. 6–Tissue magnesium concentration (C_{Mg}) and uptake rate (U_{Mg}) in 15-week-old *N. solandri* and *N. menziesii* seedlings grown at different rates of calcium, magnesium, and potassium supply in perlite and solution culture. Vertical bars indicate 2× standard error (n = 4)

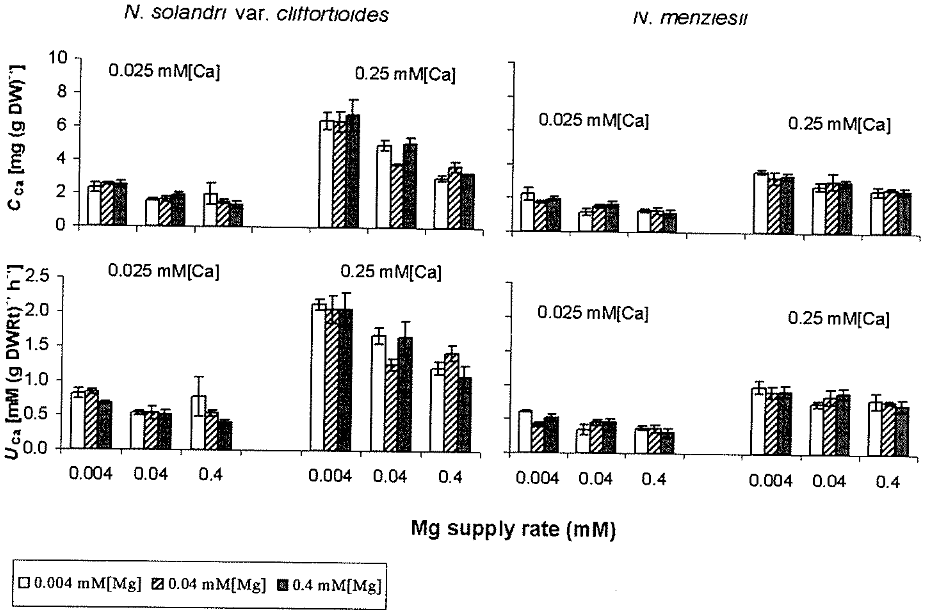

FIG. 7–Tissue calcium concentration (C_{Ca}) and uptake rate (U_{Ca}) in 15-week-old *N. solandri* and *N. menziesii* seedlings grown at different rates of calcium, magnesium, and potassium supply in perlite and solution culture. Vertical bars indicate 2× standard error (n = 4)

DISCUSSION

Soil nutrient supply plays an important role in the distribution of terrestrial plants within the limits defined by temperature and water. Optimal nutrient requirements and tolerance to supply limitation are both important factors in determining the natural distribution of forest trees in relation to soil fertility.

Both *N. solandri* and *N. menziesii* responded, in growth and nutrient uptake rates, to interactions between the rates of nitrogen and phosphorus supply. At the lowest rate of nitrogen supply, *N. solandri* grew faster than *N. menziesii* at all rates of phosphorus supply. However, under conditions with adequate or excessive nitrogen supply but deficient phosphorus supply, *N. menziesii* grew faster and was much less responsive to higher rates of phosphorus than *N. solandri*. The difference between *N. solandri* and *N. menziesii* in growth response to the rates of nitrogen and phosphorus supply is clearly related to the difference between the two species in uptake rates for nitrogen and phosphorus. *Nothofagus solandri* was more efficient in nitrogen uptake at the higher rates of nitrogen supply than *N. menziesii*. Although *N. menziesii* had noticeably greater phosphorus uptake rate at low nitrogen supply than *N. solandri*, this was likely caused by accumulation of phosphorus when seedling growth was inhibited by nitrogen supply limitation. In fact, high rates of phosphorus supply were highly toxic to seedling growth at the lowest rate of nitrogen supply (Fig. 1).

A pronounced difference in C_P was found between *N. solandri* and *N. menziesii*. Results showed that the mean C_P in *N. menziesii* was 58% greater than that in *N. solandri*. It is not clear from the present study if mycorrhizas also play a part in differentiating between the two species in phosphorus uptake. Mycorrhizal associations in root systems of plants have a strong influence on phosphorus uptake (Marschner & Dell 1994). The dependence of phosphorus uptake on mycorrhizas has been reported for *N. menziesii* (Baylis 1967). It is generally considered that all four *Nothofagus* species in New Zealand form mycorrhizal associations that are characteristically ectotrophic (Wardle 1984). It is not known, however, whether *N. solandri* and *N. menziesii* differ in their ability to form mycorrhizal associations with specific fungi that improve phosphorus uptake. Further, mycorrhizal development on root systems was not determined, and effectiveness of the inoculation may have differed between the two species.

Nothofagus solandri and *N. menziesii* were both susceptible to magnesium supply limitation. Decreasing rates of magnesium supply reduced the growth rates of both the shoots and the roots. Severe magnesium limitation resulted in development of leaf chlorosis and senescence (data not shown). The difference between *N. solandri* and *N. menzesii* seedlings is evident in this study, with *N. menziesii* showing more tolerance to severe magnesium supply limitation than *N. solandri*. Intriguingly, the two species differed in growth response to the rate of calcium supply; a moderate calcium supply limitation at 0.025 m*M* resulted in a significant reduction of shoot dry mass of *N. solandri* seedlings after 15 weeks, but had no effect on *N. menziesii*. Potassium had no apparent effect on seedling growth of the two species in the range from 0.026 to 2.6 m*M*.

Nutrient status of the growing medium affects partitioning of biomass (Clarkson & Hanson 1980), with nitrogen primarily influencing the growth of leaf area (Ingestad & Lund 1979). *RSR* in both *N. solandri* and *N. menziesii* seedlings were related inversely to the rate of nitrogen supply, which is in agreement with observations made on other forest tree species (Ingestad 1979; Ingestad & McDonald 1989; Walters & Reich 1989). The rate of phosphorus supply had no strong influence on the partitioning of biomass in *N. solandri* and *N. menziesii* seedlings.

Partitioning of biomass was also found to be influenced by the supply of calcium, magnesium, and potassium in *N. solandri*, but not in *N. menziesii*. Changes of *RSR* in response to magnesium supply in *N. solandri* resulted mainly from a substantial loss of older leaves in severely magnesium-deficient seedlings (data not shown). The *RSR* in *N. solandri* was clearly related to the rate of potassium supply, with the relationship being affected by the rate of calcium supply. Mengel & Kirkby (1987) noted that potassium enhances the translocation of photosynthates in plants. Therefore, in seedlings with potassium deficiency the translocation of photosynthates into the root systems may be inhibited, which may have contributed to the decreased *RSR* in *N. solandri* seedlings. The effect of calcium on *RSR* might result from its involvement in mediating the response of the hormonal growth regulators such as auxins, cytokinins, and gibberellins in plants (Hepler & Wayn 1985) that have detrimental effects on carbon allocation.

Our study showed that *N. solandri* seedlings were less tolerant than *N. menziesii* seedlings to supply limitations of phosphorus, magnesium, and calcium. In this study, seedlings of both species were raised from seeds collected from sites where the species occur naturally, and grown in a common environment. The differences found between the two species in mineral nutrition are clearly genetically controlled. These differences may partly reflect the soil nutrient conditions under which the two species evolved. It is also likely that the differences between the two species in response to the supply of phosphorus, calcium, and magnesium may, at least in part, contribute to the differentiated distribution patterns of *N. solandri* and *N. menziesii* in New Zealand.

Davis (1990) reported concentrations of ammonium-nitrogen, nitrate-nitrogen, calcium, and magnesium in solutions extracted by centrifugation from soils beneath five natural *Nothofagus* stands in the South Island. Nitrogen was present almost entirely as ammonium-nitrogen, and varied in concentration between 11 and 128 µmol/litre depending on site and soil depth (Table 1), 1–2 orders of magnitude below the 1780 µmol/litre found to be below optimum for growth of both *Nothofagus* species in the present study. Although conventional solution culture techniques may over-estimate limiting concentrations of ions for growth (Asher & Edwards 1978), the present results indicate *Nothofagus* stands may be commonly deficient in nitrogen, as happens with many natural ecosystems (Aerts & Chapin 2000). Calcium concentrations (11–232 µmol/litre) in the organic and upper soil layers mostly exceeded the 25 µmol/litre found to be adequate for *N. menziesii*, though concentrations at some locations and soil depths may have been limiting, especially for *N. solandri*. Concentrations of calcium in soil solutions from the natural stands were therefore at a level where the non-calcium-responsive *N. menziesii* may have had a competitive advantage over *N. solandri*. Magnesium concentrations (5–219 µmol/litre) were frequently below the level at which responses were obtained by both species in the present study. Although *N. solandri* appeared a little more responsive to magnesium than *N. menziesii*, the difference would appear to confer less of a competitive advantage over *N. solandri* than is the situation with calcium.

TABLE 1–Mean concentrations (and ranges) of ammonium-nitrogen, calcium, and magnesium in centrifuged soil solutions from beneath five natural South Island *Nothofagus* stands (from Davis 1990).

Soil layer or depth (cm)	Nutrient concentration (µmol/litre) NH_4	Ca	Mg
Organic	62 (16–126)	126 (37–242)	120 (37–219)
0–5	52 (14–128)	47 (21–101)	43 (10–108)
5–10	53 (22–104)	42 (19–92)	42 (10–73)
10–20	41 (11–80)	40 (19–88)	18 (10–42)
20–30	36 (13–80)	35 (11–73)	20 (8–56)
30–40	39 (11–68)	36 (21–66)	18 (5–50)

Our results do not support the suggestions of Adams (1976) with regard to the distribution of *Nothofagus* in relation to soil fertility. Adams (1976) compared foliar nutrient concentrations of the dominant *Nothofagus* species growing on different soils in north Westland, and concluded that species distribution, with respect to declining soil fertility, followed the order *N. fusca* > *N. menziesii* > *N. truncata* > *N. solandri*. This order was based on the assumption that high foliar nutrient concentration would indicate high fertility requirement, while low concentration would reflect low fertility requirement. It might be argued, however, that high foliar nutrient concentration could reflect an efficient uptake strategy, and an ability to tolerate nutrient supply limitation, or adaptation to low fertility soils, in which case the ordering would be opposite to that proposed. The study was based on only two stands for each species (one for *N. solandri*), and assumed that species dominance primarily reflected soil fertility status, whereas other factors, such as time since disturbance may have been important in determining species dominance. Further, stand ages varied considerably between species, and foliar nutrient concentrations have recently been shown to vary strongly with stand age in *N. solandri* (P.W.Clinton pers. comm.). In an earlier study Heine (1973) compared the nutrient concentrations of three *Nothofagus* species from a restricted sampling area (ca. 100 m^2) at one site, but did not find consistent differences between the two species in nutrient concentration: *Nothofagus menziesii* had similar or higher foliar concentrations of nitrogen, similar calcium concentrations, but lower potassium and magnesium concentrations than *N. solandri*. The natural distribution of the two species in relation to rainfall would suggest that *N. menziesii* is more tolerant of low nutrient supply than *N. solandri*. *Nothofagus menziesii* occurs in higher rainfall zones to the west of the main axial mountain ranges, and often forms pure forest with few other tree species at higher altitudes in these wetter mountain regions, whereas *N. solandri* forms extensive natural monocultures in the drier subalpine eastern regions (Wardle 1984). The two species often co-dominate towards the drier (*N. menziesii*) or wetter (*N. solandri*) ends of their respective ranges. These different distributions suggest that *N. menziesii* should be better adapted to more strongly leached soils with greater nutrient limitation than *N. solandri*. The greater leaf longevity of *N. menziesii* (Wardle 1984) might also suggest this species is better adapted to less fertile soils than *N. solandri* (Aerts & Chapin 2000). Our results support this suggestion.

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