PINUS RADIATA SEEDLING GROWTH AND MICRONUTRIENT UPTAKE IN A SAND CULTURE EXPERIMENT, AS AFFECTED BY THE FORM OF NITROGEN

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ABSTRACT

A pot trial was used to investigate the effect of the form of nitrogen (ammonium or nitrate) and the rate of nitrogen addition, at 1, 2.5, or 5 mM (14, 35, and 70 µg/ml respectively), on *Pinus radiata* D.Don seedlings grown in sand culture.

Ammonium-fed seedlings were taller and had heavier shoots and roots than nitrate-fed seedlings, particularly at the highest rate of nitrogen addition. The ammonium-fed seedlings contained greater total amounts of copper and boron and had a higher percentage of copper, boron, and iron in the shoots than nitrate-fed seedlings. The nitrate-fed seedlings contained significantly more iron.

Increasing the rate of nitrogen addition from 14 to 35 µg/ml increased shoot weights in the ammonium-fed seedlings, increased shoot height in the nitrate-fed seedlings, and increased shoot:root ratios for both forms of nitrogen. Shoot heights of ammonium-fed seedlings increased when the rate of nitrogen increased from 14 to 70 µg/ml. Within each nitrogen form, the rate of nitrogen addition did not generally affect micronutrient concentrations in the shoots or roots.

The concentrations of boron and iron (at all nitrogen rates) and copper (at 70 µg N/ml) were higher in the nitrate-fed roots than in the ammonium-fed roots but the concentrations of iron and copper (at all nitrogen rates) in the nitrate-fed shoots were significantly less than ammonium-fed shoots. The nitrate-fed roots were darker in colour and were more branched and finer than ammonium-fed roots. Organic acids, produced during nitrate reductase activity, may have a role in these differences.

Keywords: nitrogen; ammonium; nitrate; copper; zinc; boron; iron; *Pinus radiata*.

INTRODUCTION

The form of inorganic nitrogen, either ammonium or nitrate, preferentially taken up by conifers depends on a number of factors including the tree species (Nadelhoffer *et al.* 1984),

the stage of forest development and mycorrhizal associations (Attiwill & Leeper 1987), and soil characteristics, such as pH, which can affect nitrification rates (Pilbeam & Kirkby 1992). Various tree species including *Pinus contorta* Loudon (Bigg & Daniel 1978), *Pseudotsuga menziesii* (Mirb.) Franco (Van den Driessche 1971; Van den Driessche & Dangerfield 1975), and *Pinus radiata* (McFee & Stone 1968) have shown better growth in non-sterile soil-less pot trial investigations with ammonium, rather than nitrate, as the source of nitrogen. However, *P. radiata* is increasingly being grown on old pasture soils where there is a high rate of nitrate-nitrogen production (Carlyle *et al.* 1989) and where nitrate is therefore potentially the main source of available inorganic nitrogen. In a recently sampled ex-pasture soil near Rotorua, nitrate-nitrogen represented 96% of the 21 µg inorganic N/g present in the top 0 to 10 cm (S.T.Olykan, unpubl. data).

The form of inorganic nitrogen available for tree uptake can affect a number of factors relating to plant metabolic processes and nutrient dynamics, both in the soil and in the plant. For instance, the form of nitrogen influences the uptake of other plant nutrients (Pilbeam & Kirkby 1992). Studies of plant nutrition and fertilisers indicate that there can be an imbalance between nitrogen and other essential elements such as boron, sulphur, and phosphorus (Birk *et al.* 1991) where nitrate is the main nitrogen source. The form of nitrogen may also affect rhizosphere pH where plant absorption of nitrate tends to raise the rhizosphere pH, but absorbing ammonium lowers pH (Nye 1981). These pH changes will affect the concentrations of micronutrients available for plant uptake from the rhizosphere. Nitrate-fed plants require extra energy to convert the nitrate to ammonium before the nitrogen is available for plant metabolism (Binkley 1986). Raven & Smith (1976) suggested that nitrate-nitrogen nutrition also leads to the production of organic acids during nitrate reductase activity (NRA). These organic acids may bind micronutrients such as iron and reduce their activity within the plant (Haynes & Goh 1978).

To date non-soil pot trials with *P. radiata* have focused on the effect of nitrogen source on growth (Will 1961; McFee & Stone 1968; Adams & Attiwill 1982), macronutrient uptake (Will 1961; McFee & Stone 1968), and, more recently, nitrate reductase activity (Adams & Attiwill 1982). The research described here investigated the effect of the form and rate of nitrogen on the growth and micronutrient uptake of *P. radiata* seedlings grown in sand culture under controlled (glasshouse) conditions.

MATERIALS AND METHODS

Pinus radiata seed (growth and form rating GF 17) was soaked for 2 days in distilled water and then germinated in acid-washed sand. At 2 weeks of age the seedlings were planted out into pots (2.5 ℓ volume) of washed river sand, at the rate of five seedlings per pot. A fibre-glass mesh was used to prevent sand loss through pot drainage holes.

The nutrient solutions used in this study were adapted from Bigg & Daniel (1978), Adams & Attiwill (1982), and M. Andrews (pers. comm.) and were a modification of Hoagland's nutrient solution. Following the method of Adams & Attiwill (1982), the seedlings in each pot were maintained for 6 weeks in a glasshouse using a nutrient solution containing 7 µg N/ml, added as nitrate or ammonium, 1 µg P/ml, 21 µg K/ml, 5 µg Ca/ml, and 5 µg Mg/ml. The additions included sulphur and chlorine but did not contain any micronutrients as it was assumed that the seedlings contained sufficient micronutrients to sustain them for the first

2 months. No symptoms of micronutrient deficiency were observed during this period. Twice weekly, the old nutrient solution was flushed from the pots with an excess pore volume of deionised water and replaced with 600 ml of fresh nutrient solution.

It was assumed that because the solutions were replaced twice weekly the chance of significant nitrification occurring was largely eliminated despite non-sterility of the medium. The seedlings were not inoculated with mycorrhizal fungi.

At 2 months of age the seedlings received one of six full nutrient solutions which differed in the source of nitrogen added (as ammonium or nitrate) and in the rate of nitrogen addition at 14, 35, or 70 μg N/ml (N14, N35, and N70 in the text) equivalent to 1, 2.5, or 5 mM N. Sulphur additions also varied between 66 and 226 μg/ml. The other added nutrients were phosphorus, potassium, calcium, magnesium, copper, zinc, boron, manganese, molybdenum, cobalt, iron, chloride (106 μg Cl/ml), and sodium (1 μg Na/ml) which were all added at the same rate to each pot (*see* Appendix 1). There were three replicates of each treatment, with the nutrient solutions being replaced twice a week as before. The pH of the added nutrient solutions ranged from 6.2 to 6.4 at each application.

Seedling harvest occurred at 6 months of age. Shoots and roots were separated and the roots were washed to remove excess sand, and dried. Individual shoot heights were measured and then the shoots and the roots were combined to give two bulk samples per pot. The samples were then dried (60°C), weighed, and ground to pass a 1-mm sieve.

The concentrations of micronutrients were determined by dry-ashing at 600°C for 1 hour, with the ash being extracted in 10 ml of 0.5M H_2SO_4. The filtered (Whatman 40) solution was analysed for copper, zinc, and iron contents by atomic absorption spectrophotometry and for boron using the azomethine-H technique (Wolf 1974; Gaines & Mitchell 1979).

Data were subjected to analysis of variance (ANOVA) using the computer program GENSTAT. The following effects were examined: (i) the effect of the increasing rates of nitrogen form (ammonium or nitrate) addition, and interactions between nitrogen form and rate, on seedling shoot and root dry weights, shoot dry weight to root dry weight (shoot:root) ratios, and seedling height, and (ii) the effect of the increasing rates of nitrogen form (ammonium or nitrate) addition, and interactions between nitrogen form and rate, on micronutrient concentrations in the shoots and roots, total micronutrient uptake by the seedlings, and the percentage of total micronutrients in the seedling shoots.

The least significant difference (LSD) test was used to compare mean values at the 5% level.

The addition of sulphur in the nutrient solutions varied, ranging between 66 and 226 μg/ml. Although sulphur was considered to be a "non-treatment" nutrient, the possible effect of sulphur on seedling growth and nutrient characteristics was not statistically analysed as it was associated with the addition of both ammonium-nitrogen and potassium.

RESULTS
Seedling Growth
The shoot component represented 70 to 80% of the total seedling dry weight per pot (Fig. 1). Shoot dry weight was significantly affected by the form (p<0.001) and the rate of nitrogen addition (p=0.002). The ammonium-fed shoots were significantly (p<0.05) heavier
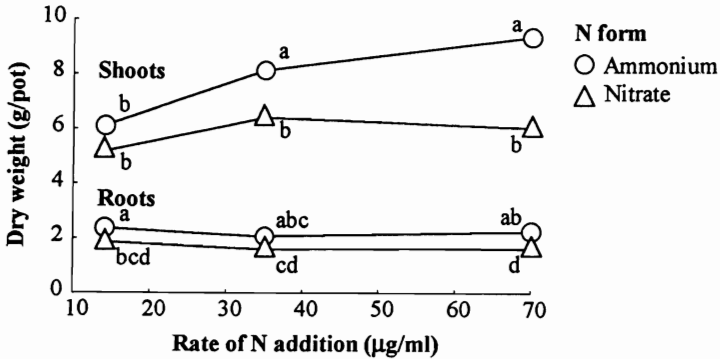
FIG. 1–Effect of nitrogen form and rate on the dry weight of *P. radiata* seedling shoots and roots. Shoot or root means with the same letter were not significantly different (p<0.05).

than the nitrate-fed shoots at N35 and N70. The rate of nitrate-nitrogen addition did not significantly affect shoot weights which ranged from 5.2 g/pot (N14) to 6.4 g/pot (N35). Increasing the rate of ammonium-nitrogen addition from 14 to 35 μg/ml significantly increased shoot weights. At N35 and N70 ammonium-fed shoot weights were 8.2 and 9.4 g/pot respectively, compared with 6.1 g/pot at N14.

The form of nitrogen also had a significant (p=0.002) effect on root dry weight. The ammonium-fed roots were significantly (p<0.05) heavier than the nitrate-fed roots at N14 (2.4 *v.* 1.9 g/pot) and N70 (2.2 *v.* 1.6 g/pot). Within each form of nitrogen, increasing the rate of nitrogen addition had no significant effect on root weight.

Shoot height was significantly affected by the form (p<0.001) and the rate (p=0.016) of nitrogen addition. The ammonium-fed seedlings were taller than the nitrate-fed seedlings only in the N70 rate (Fig. 2). With an increase in the rate of ammonium-nitrogen from N14 to N70, seedling height significantly increased from 26.5 to 29.1 cm. For the nitrate-fed
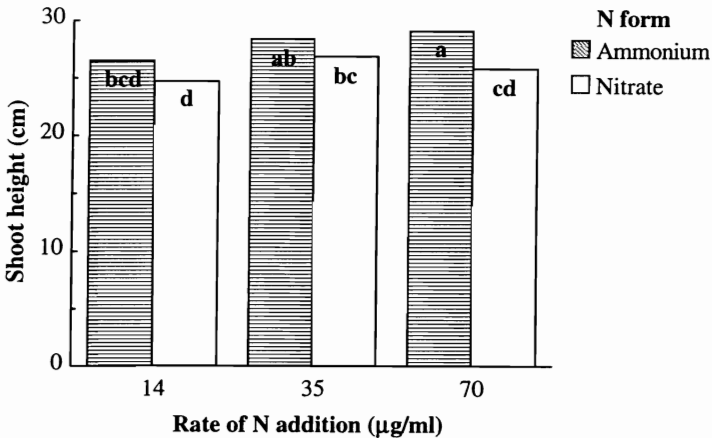

FIG. 2–Effect of nitrogen form and rate on *P. radiata* seedling shoot height. Means with the same letter were not significantly different (p<0.05).

seedlings, shoot height significantly increased from N14 to N35 (24.7 to 26.9 cm). The N70 ammonium-fed seedlings were significantly ($p<0.05$) taller than all of the nitrate-fed seedlings.

The shoot:root ratios for each pot were significantly affected by the rate of nitrogen addition ($p<0.001$) (Fig. 3). The addition of N35 resulted in a significantly higher shoot:root ratio, with a mean of 3.8 compared to 2.7 for the N14 treatment. Increasing the rate of nitrogen from 35 to 70 µg/ml did not result in further increases in the shoot:root ratio. The form of nitrogen had no effect on the shoot:root ratio.
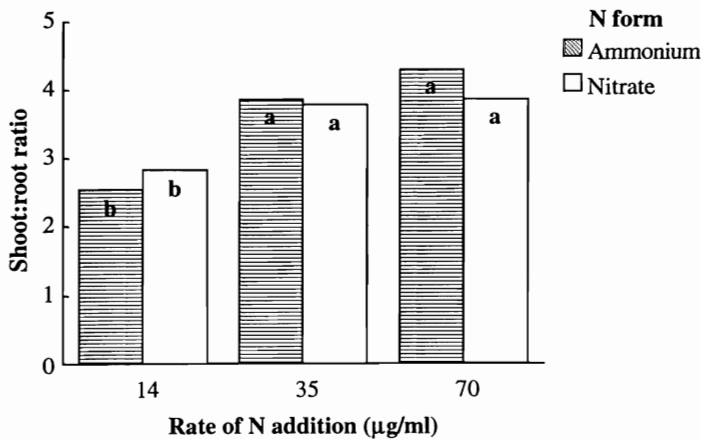

FIG. 3–Effect of nitrogen form and rate on shoot:root dry weight ratios of *P. radiata* seedlings. Means with the same letter were not significantly different ($p<0.05$).

Nutrient Concentrations

Concentrations of copper, zinc, and iron were higher in the roots than in the shoots (Table 1). In contrast, boron concentrations were higher in the shoots. Neither the form nor the rate of nitrogen addition significantly affected the shoot or root concentrations of zinc. The form of nitrogen significantly affected ($p<0.001$) the shoot concentrations of copper and iron which were significantly higher ($p<0.05$) in the ammonium-fed shoots. The form of nitrogen significantly affected ($p=0.010$) shoot concentrations of boron but there were no significant differences between the forms of nitrogen for each rate of addition. Shoot concentrations were not affected by increasing rate of nitrogen, addition except for iron which increased significantly ($p=0.007$) from 25.8 µg/g at N14 to 32.2 µg/g at N35 when ammonium was the form of nitrogen applied.

The form of nitrogen significantly affected the root concentrations of copper ($p=0.012$) and boron and iron ($p<0.001$) with the concentrations of boron and iron being significantly higher in the nitrate-fed roots for all rates of nitrogen addition. The rate of nitrogen addition significantly affected ($p=0.034$) the root concentrations of iron but only when nitrogen was in the nitrate form. Significantly higher iron concentrations were associated with an increase in nitrate from N14 to N35 but a further increase to N70 had no effect. The interaction between nitrogen form and rate significantly affected ($p=0.018$) copper in the roots. For the N14 and N35 rates, there was no difference in the concentration of copper in the roots

TABLE 1–Effect of nitrogen form and rate on micronutrient concentrations of *P. radiata* seedling shoots and roots. For each nutrient in the shoots or roots, values followed by the same letter were not significantly different at the 5% level.

Nutrient (μg/g)	Nitrogen form	Shoots			Roots		
		N14	N35	N70	N14	N35	N70
Cu	Ammonium	5.0 a	5.7 a	5.0 a	9.0 b	9.3 b	7.3 b
	Nitrate	3.5 b	3.3 b	3.8 b	9.0 b	11.0 b	17.8 a
Zn	Ammonium	21.1 a	21.0 a	17.9 a	148 a	227 a	150 a
	Nitrate	23.4 a	20.8 a	22.6 a	128 a	193 a	166 a
B	Ammonium	26.2 ab	26.3 ab	26.4 a	10.3 b	10.7 b	9.8 b
	Nitrate	22.5 ab	21.3 b	22.8 ab	18.6 a	18.3 a	19.4 a
Fe	Ammonium	25.8 b	32.2 a	29.5 a	195 c	189 c	204 c
	Nitrate	19.1 c	21.5 c	21.1 c	372 b	427 a	466 a

between the two forms of nitrogen. However, at N70 the concentrations of copper in the nitrate-fed roots were higher than in the ammonium-fed roots and also higher than when nitrate was added at N14 and N35.

Total Micronutrient Uptake and Partitioning

Total uptake of copper and boron (Table 2) was significantly (p<0.05) greater in the ammonium-fed seedlings but total iron uptake was significantly (p<0.05) higher in the nitrate-fed seedlings. For both copper and boron, the difference in total uptake between the forms of nitrogen was a result of significantly more copper and boron in the ammonium-fed shoots. Although nitrogen form had no effect on the amount of copper in the roots, there was significantly more boron in the nitrate-fed roots. In contrast, the relatively large amount of iron in the nitrate-fed roots contributed to the significantly greater total iron uptake for this nitrogen form. However, the amount of iron in the nitrate-fed shoots was about half of that in the ammonium-fed shoots.

The greater proportion of total boron uptake was into the shoots of the *P. radiata* seedlings but zinc and iron uptake was predominantly into the roots (Table 2). The form of nitrogen

TABLE 2–Effect of nitrogen form on total micronutrient uptake, micronutrient uptake into the shoots and roots, and the percentage of total micronutrient in the shoots of *P. radiata* seedlings. For each nutrient, values for total, shoots, roots, or percentage in shoot followed by the same letter were not significantly different at the 5% level.

Nutrient	Nitrogen form	Total (μg/pot)	Shoots (μg/pot)	Roots (μg/pot)	Percentage in shoot
Cu	Ammonium	60 a	41 a	19 a	68 a
	Nitrate	42 b	21 b	21 a	51 b
Zn	Ammonium	554 a	157 a	397 a	30 a
	Nitrate	403 a	129 a	274 a	34 a
B	Ammonium	232 a	209 a	24 b	90 a
	Nitrate	163 b	131 b	32 a	80 b
Fe	Ammonium	675 b	234 a	441 b	34 a
	Nitrate	840 a	122 b	718 a	15 b

significantly affected (p<0.001) the percentages of total of copper, boron, and iron uptake in the shoots which were higher in the ammonium-fed seedlings. The uptake and partitioning of zinc was not affected by the form of nitrogen.

DISCUSSION

The rate and particularly the form of nitrogen addition affected *P. radiata* seedling growth and micronutrient concentrations and uptake. Nitrogen fertiliser increases the biomass of young *P. radiata* trees (Nambiar & Fife 1987). This effect can be modified by the form of nitrogen as nitrate or ammonium, and *P. radiata* seedlings grow better with an ammonium-nitrogen form (Ryan, cited by Turner & Lambert 1991; McFee & Stone 1968) regardless of the rate of addition (McFee & Stone 1968). However, Adams & Attiwill (1982) found no significant difference in the shoot and root dry weights of nitrate- or ammonium-fed mycorrhizal-infected *P. radiata* seedlings.

In this study, the ammonium-fed seedlings were heavier than the nitrate-fed seedlings in the N35 and N70 rates and were taller in the N70 rate. These results confirm that non-mycorrhizal *P. radiata* grows better with an ammonium-nitrogen form in a controlled environment. However, the seedlings were able to grow satisfactorily with high rates of nitrate-nitrogen, although shoot and root weights did not increase with an increase in nitrate addition while shoot heights increased from N14 to N35. The optimum rates of nitrogen addition, from a growth point of view, were N35 for the nitrate-fed seedlings (based on shoot height only) and N35 and N70 for the ammonium-fed seedlings.

The effect of nitrogen form on seedling size observed here may be related to the extra energy required to reduce nitrate-nitrogen to ammonium-nitrogen within the plant (Binkley 1986). In our pot experiment nitrogen uptake was significantly correlated (p<0.01) with total seedling weight and height. The nitrate-fed seedlings had a lower total nitrogen uptake and were smaller, in both weight and height, than the ammonium-fed seedlings (particularly at N70). According to Pilbeam & Kirkby (1992) the assimilation of the nitrate ion by plants is metabolically more expensive than ammonium. Adams & Attiwill (1982) suggested that, once absorbed, ammonium-nitrogen may be metabolised more rapidly than nitrate-nitrogen.

A shift in biomass production from the roots to the shoots can be expected after application of nitrogen fertiliser (Will 1974, cited by Barker 1978). Increasing the rate of nitrogen addition from N14 to N35 increased the shoot biomass and, without a corresponding increase in the root biomass, resulted in a significantly higher shoot:root ratio. It appears that the allocation of biomass between the seedling shoots and roots is related to total nitrogen uptake which significantly (p<0.05) increased as the rate of nitrogen addition increased from N14 to N35 for both nitrogen forms (data not shown). With the provision of full nutrient solutions during the pot trial, this change in shoot:root ratios did not appear to disadvantage the N35 and N70 seedlings.

Adams & Attiwill (1982) reported a shoot:root ratio of 1.3 with nitrogen added at 42 μg/ml. This value is lower than the shoot:root ratios of 2.5 to 4.3 for the N14 to N70 rates, respectively, in this experiment. In the field, high shoot:root ratios of 5 have been found for *P. radiata* seedlings (Nambiar 1980) and high rates of toppling have been noted in young *P.radiata* trees growing in highly fertile soils (Chavasse 1969). As noted by Mason (1985), the root system of a tree provides the means to absorb soil water and nutrients as well as

anchorage. In the field, the development of high shoot:root ratios in response to high amounts of soil nitrogen, as found in agroforestry and ex-pasture systems, may affect the ability of the tree root system to support its proportionally much larger above-ground biomass as well as reduce the potential exploitation of the soil volume for nutrients.

Previous studies have highlighted the effect of nitrogen form on the cation-anion balance of macronutrients (Turner & Lambert 1991) where a nitrate form typically stimulates cation uptake and inhibits anion uptake (Haynes 1986). There were significant differences in the concentrations of micronutrients in the seedlings according to which form of nitrogen had been added. Iron concentrations were higher in the nitrate-fed roots and total iron uptake was also higher in the smaller nitrate-fed seedlings. However, with copper and zinc there were no clear differences between the nitrogen forms. While this evidence did not clearly support the idea of increased micronutrient-cation uptake with nitrate-nitrogen, the concentrations of magnesium in the shoots and roots and calcium in the roots of the nitrate-fed seedlings were higher at all rates of nitrogen than in the ammonium-fed seedlings (Olykan 1993). The concentrations of calcium were higher in the nitrate-N70 shoots. These results suggest that macronutrient cations may be more important in the cation-anion balance than micronutrient cations when nitrate is the form of nitrogen.

The percentage of total of copper, iron, and boron uptake was significantly higher in the ammonium-fed than the nitrate-fed shoots (Table 2), with the percentage of all three nutrients increasing significantly as the rates of ammonium addition increased from N14 and N35 (Olykan 1993). The increased uptake was due mainly to the greater shoot biomass in these treatments but the concentrations of copper and iron were also significantly higher in the ammonium-fed shoots. In the nitrate-fed roots there was higher uptake of iron and boron particularly, but also copper at N70, than in the ammonium-fed roots. The significantly lower percentage of these micronutrients in the nitrate-fed shoots suggests that there may be some mechanism preventing their transport from the roots to the shoots. It has been noted that the reduction of nitrate-nitrogen to ammonium-nitrogen can occur in the roots (Binkley 1986). Adams & Attiwill (1982) detected NRA in the roots, and not the needles, of *P. radiata* seedlings grown in sand culture, and the NRA increased with increasing rates of nitrate addition. During the reduction of nitrate a surplus of cations develops which is balanced by the synthesis of organic acid anions (Raven & Smith 1976) such as malate and citrate (Haynes & Goh 1978). For some conifers, nitrate nutrition can result in high levels of organic acids and symptoms of iron deficiency because iron may be bound to these organic acids, thus reducing its activity in the plant (Haynes & Goh 1978). This induced deficiency mechanism may also occur for other trace elements. Previous studies have found that greater nitrate availability can result in higher accumulations of magnesium, manganese, iron, and aluminium in the roots, not necessarily in proportion to that translocated to the crown (Ryan, cited by Turner & Lambert 1991). The inhibition of iron, and possibly copper and boron, movement to the shoots of the nitrate-fed seedlings may be related to the binding of these trace elements with organic acids reducing their transport to the shoot and therefore increasing their storage within the root system.

A difference in colour and morphology was observed between the roots of the ammonium- and nitrate-fed seedlings. The nitrate-fed roots were darker, regardless of the rate of nitrogen addition, and were more branched and more finely branched than the ammonium-fed roots. Bigg & Daniel (1978) also found that roots of *Pinus contorta* and *Picea engelmannii* (Parry)

Engelm. were darker, and sometimes the entire root system was almost black, when grown in nitrate. They noted that this had been identified in the roots of other plant species.

There appear to be a number of possible reasons for the darkened nitrate-fed roots. For instance, Hacskaylo *et al.* (1969, cited by Bigg & Daniel 1978) described the dark roots of *Pinus sylvestris* L. as being a symptom of nitrogen deficiency. While the pot trial results (Olykan 1993) indicated that the concentration of nitrogen in the nitrate-fed roots, at 14 g/kg, was significantly (p<0.05) lower than the 17 g/kg in the ammonium-fed roots, the concentrations of nitrogen in the shoots appeared to be adequate, at 18 to 19 g/kg respectively, and the seedlings were not visibly suffering from a nitrogen deficiency. The pot trial results also indicated that there was an increase in micronutrient concentrations, particularly iron, in the roots of the nitrate-fed seedlings. Chaney & Bell (1987) found that roots grown with FeEDTA and nitrate-nitrogen became covered with hydrous iron oxides (dark in colour) and suggested that other iron chelates such as FeEDDHA and FeHEDTA could be used, depending on the plant species. It is also possible that manganese (and/or other unmeasured micronutrients) may have affected the growth and root morphology of the nitrate-fed seedlings.

CONCLUSIONS

This pot trial confirmed that the form of nitrogen—either as ammonium or as nitrate—can significantly affect non-mycorrhizal *P. radiata* seedling shoot and root weight and height, as well as micronutrient concentrations, uptake, and the percentage of total micronutrient in the shoots

Ammonium-fed seedlings were taller than nitrate-fed seedlings at the N70 rate, and had heavier shoots (at N35 and N70) and roots (at N14 and N70).

While the cation-anion balance during nitrate uptake appeared to have the greatest positive effect on the macronutrient cations calcium and magnesium, iron uptake was also increased compared to ammonium-fed seedlings. However, differences in the uptake of copper did not appear to be a result of changes in the cation-anion balance.

The lower total amounts of copper and boron in the nitrate-fed seedlings were probably a result of their smaller size rather than an interference in the uptake of these micronutrients. However, it is possible that once nutrients such as copper and iron have been taken up by nitrate-fed seedlings, they may become bound to organic acids produced during the assimilation of nitrate. As a result, their transport to the shoot could be significantly reduced, explaining the lower concentrations of copper and iron in the nitrate-fed shoots and an increase in the concentrations of copper (at N70) and iron (at all nitrogen rates) in the roots of nitrate-fed compared with ammonium-fed seedlings. Boron concentrations were also elevated in the nitrate-fed roots but shoot concentrations did not differ from those in the ammonium-fed shoots.

These results have implications for the growth of *P. radiata* on ex-pasture sites where nitrate may be the predominant nitrogen form and/or nitrogen is present at high levels. With the increase in the shoot:root ratio at high nitrogen levels and the possible prevention of micronutrient movement from the roots to the shoots where nitrate is the predominant form of nitrogen, the tree's ability to absorb nutrients, particularly micronutrients and those nutrients at low levels in the soil, may be reduced and/or may not meet the demands of fast-

growing *P. radiata* trees. However, the contribution of other factors to micronutrient uptake, such as changes in rhizosphere pH, mycorrhizal associations, and mixtures of ammonium and nitrate, need to be considered as well.

ACKNOWLEDGMENTS

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APPENDIX 1

NUTRIENT CONCENTRATIONS PRESENT IN EACH TREATMENT OF THE SAND-CULTURE POT TRIAL WITH *P.RADIATA* SEEDLINGS

Nutrient	Rate (µg/ml)	Treatment No.	Compound	Other nutrients added (µg/ml)
Macronutrients				
NH_4^+-N	14	1	$(NH_4)_2SO_4$	S = 16.0
	35	2		40.1
	70	3		80.2
NO_3^--N	14	4	KNO_3	K = 39.1
	35	5		97.8
	70	6		195.5
P	8	All	KH_2PO_4	K = 10.1
K	97.7	5	K_2SO_4	S = 40.1
	156.4	4		64.1
	195.5	1,2,3		80.1
Ca	60	All	$CaCl_2.6H_2O$	Cl =106.2
Mg	50	All	$MgSO_4.7H_2O$	S = 66
Micronutrients				
Cu	0.01	All	$CuCl_2.2H_2O$	Cl = 0.011
Zn	0.01	All	$ZnCl_2$	Cl = 0.011
B	0.1	All	$Na_2B_4O_7.10H_2O$	Na = 0.106
Mn	0.125	All	$MnCl_2.4H_2O$	Cl = 0.161
Mo	0.003	All	$Na_2MoO_4.2H_2O$	Na = 0.0014
Co	0.1	All	$CoSO_4.7H_2O$	S = 0.054
Fe	2	All	EDTAFeNa	Na = 0.82