MAGNESIUM NUTRITION AND DRY MATTER ALLOCATION PATTERNS IN *PINUS RADIATA*

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ABSTRACT

Pinus radiata D. Don seedlings grown in a range of magnesium solution concentrations showed differences in root : shoot ratios, with those exhibiting magnesium deficiency symptoms allocating proportionately less resources to the roots than healthy seedlings. A foliar spray of 2% magnesium solution with 0.2% Pulse™ in water alleviated the deficiency symptoms and improved dry matter allocation to the roots. In a 7-year-old *P. radiata* fertiliser trial, magnesium fertiliser treatments caused no improvement in basal area or height after 6 years but foliar magnesium concentrations had been raised above the critical level. Trees with adequate foliar magnesium had nearly double the fine root biomass of those with inadequate concentrations. This suggested that below-ground dry matter allocation was decreased in deficient trees, and that the noted slow growth response of *P. radiata* to magnesium fertiliser may be due to the need to rebuild the root system before an above-ground response occurs. However, while fine root (<1 mm) biomass was increased in 3-year-old trees treated 18 months previously with magnesium fertiliser, no relationship between root:shoot ratio and magnesium application was found. It was suggested that the changes in root:shoot ratio may develop over a period longer than 3 years.

Keywords: magnesium; root:shoot ratio; tree nutrition; *Pinus radiata.*

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INTRODUCTION

Magnesium deficiency in *P. radiata* is receiving increasing attention in New Zealand forestry. Deficiency symptoms occur nationally, with the most strongly affected areas in the central North Island, Westland, Otago, Southland, and Nelson (Hunter *et al.* 1991). Although fertiliser can be effective in correcting the deficiency and improving growth, response is often slow, commonly with a gradual increase in foliar magnesium concentration followed by an improvement in growth when concentrations are above Will's (1985) critical level of 1.0 mg/g. Possible reasons for this slow response include slow solubility of fertiliser source, competitive influence of understorey vegetation, and physiological attributes of the tree. The study reported here concentrated on physiological aspects of magnesium deficiency, in particular dry matter allocation patterns between roots and shoots.

Magnesium is a critical component in the carbon fixation and transformation processes in the tree. Lower photosynthesis rates alone are less important for growth in magnesium-deficient Norway spruce (*Picea abies* (L.) Karsten) than a combination of lower photosynthesis rate and disruption of transformation processes following initial carbon fixation (Oren *et al.* 1988a, b). But Ericsson (1991) found the main constraint associated with magnesium deficiency in birch (*Betula pendula* Roth.) was carbon fixation, with impaired transport to the root playing only a minor role in the system. Shear (1980) stated that the first sign of magnesium deficiency in fruit trees is a breakdown of the feeding-root system, and stressed the importance of maintaining an adequate supply of magnesium to the tree.

Impaired movement of photosynthate to the root system has strong significance for nutrient uptake by the tree. It is generally accepted that plants deficient in nitrogen and phosphorus put more energy into their root systems, increasing their root:shoot ratios (Linder & Rook 1984). This allows the plant to exploit a greater soil volume and improves uptake of the element in short supply. Ericsson (1991) has shown the opposite to be true with magnesium in birch. A decrease in the root:shoot ratio was measured when trees were grown at sub-optimal levels of magnesium. This accords with the findings of Matzner *et al.* (1985) and also Marschner (1986) and Shear (1980). However, root: shoot ratios derived from data presented by Will (1961) where *P. radiata* was grown under a range of magnesium concentrations suggested an increase in root:shoot ratio with increasing degree of deficiency. It was not possible to statistically analyse this information, and so the results can only be considered indicative. Calculation of root:shoot ratio from biomass data presented by Hunter *et al.* (1986) indicated no change between trees treated with fertiliser and those without, although that study did not include roots less than 5 mm in diameter (J.A.C.Hunter-Smith pers. comm).

Two consequences of the decrease in carbon allocation to the roots are likely. Firstly, the tree's root system may be smaller, allowing less magnesium uptake by the tree, due both to the roots exploiting a smaller soil volume, and to limitations on the rate of uptake caused by the smaller root surface area. Secondly, the decreased carbon allocation to the roots will provide less substrate for the mycorrhizal symbiosis which is so important in pines (Bowen 1984). Mycorrhizas are generally recognised as being most critical for phosphorus uptake with its very low rate of diffusion. However, they are also likely to be important for other elements where soil solution concentrations are low and movement to the root is primarily by diffusion. Decreased mycorrhizal activity will lead to a smaller volume of soil being exploited by fungal hyphae and less magnesium being assimilated by the tree (Bowen 1984).

Where the root systems of magnesium-deficient trees have declined, this could affect the rate of response of trees to applied fertilisers. The movement of the magnesium to the root by diffusion in the soil solution would be slower as the rooting density is lower. Also, if the root's uptake capacity (I_{max}) is exceeded there will be a limit to the uptake rate of magnesium, as uptake is then a direct function of the root surface area.

The objective of this study was to determine whether different levels of magnesium supply affected root biomass and dry matter allocation patterns between roots and shoots of *P. radiata* in both seedlings and mature trees.

MATERIALS AND METHODS

Glasshouse Solution Culture Experiment

Three concentrations of magnesium (0.2, 1.0, and 10.0 mg Mg/ℓ in solution) were tested on tree growth and dry matter allocation to the roots and shoots of potted seedlings. The experiment began with 15 replicates of the three soil solution levels, in a completely randomised design. Each 4-ℓ pot contained two *P. radiata* seedlings inoculated with *Suillus luteus* (L. ex Fr.) S.F. Gray mycorrhizal fungus and planted in perlite. The magnesium was applied with a background of Ingestad's solution (Ingestad 1971) found optimum for birch (*Betula verrucosa* Ehrh.), with a nitrogen concentration of 100 mg/ℓ and pH adjusted to 5.0. Nutrient solutions were added to keep each pot at field capacity, and pots were flushed with fresh solution three times per week.

Mean day/night temperatures in the glasshouse were 26°/15°C, and day length was 16 hours. After 95 days five replicates of each treatment were harvested. Tree heights were measured, and the tops were cut off at the perlite surface. Roots were washed clean of perlite and clipped from the remaining stump, and root length was measured using Newman's line intersection technique (Bohm 1979). Plant samples were dried at 70°C. Root (<2 mm diameter), stump, and shoot weights were recorded and root:shoot ratios (<2 mm root weight / shoot weight) calculated. The stump was included as part of the shoot for these calculations. Dried samples were ground in a ring mill and total magnesium concentration of the samples was analysed on an acid digest using atomic absorption spectroscopy (Nicholson 1984).

After the harvest at day 95, the remaining 10 replicates for each treatment were randomly assigned to two groups of five replicates each. A foliage spray of 2% $MgSO_4$ with 0.2% Pulse™ surfactant (an organo-silicone co-polymer) was applied three times per week for 1 month to one group, with care that the spray did not reach the perlite. The second group was not treated with the foliar spray. Nutrient solution applications to the perlite continued as before. After a further 76 days all plants were harvested and processed using the same methods as the first harvest, except that after the plants were removed from the pots and washed clean of perlite, the roots were then clipped directly from the stem so there was no stump component in this harvest. Root weights were recorded but root length was not measured.

Field Studies

Kaingaroa root study

The effect of magnesium fertiliser on dry matter allocation patterns was investigated at two sites. The first site was a Forest Research Institute magnesium fertiliser trial in

Compartment 873 of Kaingaroa Forest, in the central North Island. The stand had been planted in 1983 at a stocking of 1667 stems/ha and the fertiliser trial was established a year later. The stand was thinned to 550 stems/ha in August 1990. The site was on Kaingaroa sand and had previously been a firebreak. The trial design was a randomised block with ten 20 × 50-m plots. Fertiliser treatments applied were 0, 25, 55, 150, and 400 kg Mg/ha as dolomite, with two replicates. Foliar magnesium concentration in the control plots 3 months after fertiliser application was 0.69 mg/g, indicating magnesium deficiency. By March 1990 trees in plots treated with 0 and 400 kg Mg/ha had very different foliar magnesium concentrations (0.71 mg/g and 1.50 mg/g respectively) although there were no significant differences in height (4.78 m and 4.82 m respectively) or basal area (51.4 m^2/ha and 52.2 m^2/ha respectively) measured in 1989.

Root sampling was done at the trial in August 1990. A preliminary field assessment indicated the roots had occupied the entire site and the smaller roots (<5 mm) were evenly distributed over the plots. Eight soil cores of 15 × 15 cm area and 20 cm depth were taken randomly from each of the control plots and those treated with 400 kg Mg/ha. After an initial separation of roots from the soil on site, the roots were washed through sieves and separated into <1 mm, 1–2 mm, and >2 mm diameter fractions; root lengths for each fraction were determined using Newman's line intersection technique (Bohm 1979). Mycorrhizal infection was qualitatively assessed as abundant or not abundant. The samples were dried at 70°C and the dry weights recorded.

Tauhara biomass study

The second site was at Halls block in Tauhara Forest, 15 km north-east of Taupo in the central North Island, where an experiment had been installed to investigate the effects of magnesium, grass, and boron on tree growth and magnesium uptake. The site was planted in winter 1988 at a stocking of 2145 stems/ha. Plots of 7 × 20 m were installed in September 1989 in a 3^2 factorial with treatments of magnesium (0 and 400 kg Mg/ha as Epsom salts), boron (0 and 4 kg B/ha as boric acid), and perennial rye grass (*Lolium perenne* L.) (0 and 100% cover), with four replicates. Treatments were applied in September; fertiliser was applied by hand, the ryegrass was sown on the 100% cover plots, and weed-free conditions were maintained on the 0% cover plots by periodic applications of herbicide where necessary.

In March 1991 tree biomass was estimated from all replicates of the following four treatments: 0 Mg, 100% grass cover (control); 0 Mg, 0 grass cover; 400 kg Mg, 100% grass cover; 400 kg Mg, 0 grass cover. Four replicates of each treatment were sampled except for the control where only one replicate could be sampled due to time constraints on the field work.

A stratified random sampling strategy was used. One tree was selected randomly from each of three volume index (d^2h) classes (small, medium, and large) within each plot (Madgwick 1981), felled, and divided into foliage (all ages combined), branches, and stem. Fresh weights were recorded in the field. Approximately 2-kg sub-samples were taken of foliage and branches; the stem was sub-sampled by cutting 2-cm discs at 20-cm intervals down the stem and combining the discs for drying. Tree stumps were excavated and roots severed at the stump. Sub-samples were taken to the laboratory to be dried and weighed and

results (kg/ha) were obtained by converting the results for the three trees sampled to plot means using the basal area ratio method of Madgwick (1981).

Tree roots were sampled in all four replicates of the four treatments. Soil cores of 15 × 15 cm area and 20 cm depth were taken in random directions from four inner plot trees, at two distances, 30 cm and 100 cm from the trunk, yielding a total of eight samples per plot. Tree roots were separated from the soil in the field, bagged, and removed to the laboratory for further processing. Roots were washed through sieves and separated into four diameter classes: >5 mm, 2–5 mm, 1–2 mm, and <1 mm. Root lengths were measured for each diameter class using Newman's line intersect technique (Bohm 1979). Results were expressed as centimetres per cubic centimetre soil (L_V). Root biomass was calculated as plot means (kg/ha) by weighting the samples according to distance from the trunk and hence area of the plot the samples represented. Samples taken at the 30 cm distance were representative of 8.256% of the total plot area and those taken at 100 cm represented the remaining plot area (91.743%). Weighted means were calculated based on these percentages. Mycorrhizal root tips were counted on a sub-sample of each root sample and expressed as number per cubic centimetre of soil. Root:shoot ratios were calculated for each plot based on total above-ground biomass, including stump (kg/ha) and total root biomass (kg/ha).

Composite samples of mature current year's foliage were collected from primary branches in the top third of the crown of all inner plot trees (between 10 and 15 trees per plot). Samples were dried at 70°C, ground in a ring mill, and analysed for magnesium by X-ray fluorescence. The foliar magnesium concentrations were used to rank treatments in order of magnesium deficiency.

Statistical Analysis

Analysis of variance and regression analysis were used to evaluate the results using the SAS statistical package (SAS Institute 1985).

RESULTS

Effect of Solution Magnesium Concentration on Seedling Growth and Root:Shoot Ratio

The magnesium treatments strongly affected growth and magnesium status, with seedlings grown in 0.2 mg/ℓ and 1.0 mg/ℓ magnesium solution showing pronounced deficiency symptoms. Mean magnesium concentrations for the whole plants were 0.27 mg/g, 0.35 mg/g, and 1.28 mg/g for the 0.2, 1.0, and 10.0 mg/ℓ treatments respectively. Seedlings in the 10.0 mg/ℓ treatment were healthy, but the other seedlings showed obvious deficiency symptoms.

Growth and biomass data (Table 1) showed increasing tree height and weight with increasing magnesium concentration. Treatment effects on height and weight were strongly significant ($p=0.0001$). Root:shoot ratios were also affected by treatment ($p=0.0334$) with the deficient seedlings having a lower allocation of dry matter to the root system than the healthy seedlings, though the difference between the 0.2 mg/ℓ and the 1.0 mg/ℓ treatments was not significant.

After the foliar spray treatment, the deficient seedlings generally showed a marked improvement in growth within 1 to 2 weeks, with a disappearance of deficiency symptoms.

TABLE 1–Effects of solution magnesium concentration on growth, biomass, and root:shoot ratio of seedlings grown in perlite medium for 95 days.

Magnesium (mg/*l*)	Height (cm)	Top weight	Root weight	Biomass	Root:shoot ratio
		(g/pot)			
0.2	7.8	0.86	0.28	1.15	0.326
1.0	11.8	2.08	0.67	2.75	0.321
10.0	20.3	4.65	1.99	6.65	0.433
Source of variation			Probability > F		
Mg	0.0001	0.0001	0.0001	0.0001	0.0334

Some seedlings in the 0.2 mg/ℓ treatment did not respond as they had a very small percentage of live needles remaining by this stage. In addition to this, continued spraying of the foliage in the 10 mg/ℓ treatment caused scorching of the foliage and a suppression of growth. When the experiment was analysed as a whole there were no overall significant effects of foliar spray on the root:shoot ratio, probably because of aforementioned problems. However, differences were apparent in the 1.0 mg/ℓ treatment which was unaffected by inclusion of biomass data from dead seedlings or those with needle scorching. Results for this treatment are shown separately in Table 2. There were large improvements in growth, and an overall improvement in root:shoot ratio after application of magnesium to the foliage, as proportionately more of the biomass response was allocated to the roots.

TABLE 2–Effect of a 2% magnesium solution applied to foliage of seedlings grown in perlite medium with a 1.0 mg Mg/*l* solution concentration, 76 days after initial treatment application.

Treatment	Height (cm)	Top weight	Root weight	Biomass	Root:shoot ratio
		(g/pot)			
+ foliar Mg	29.1	23.53	6.99	30.52	0.290
0 foliar Mg	20.5	11.49	2.29	13.79	0.194
Source of variation			Probability > F		
foliar Mg	0.0090	0.0099	0.0092	0.0092	0.0224

Effect of Magnesium Deficiency on Root Length and Biomass, Kaingaroa Forest

The data from the sampling at Kaingaroa (Table 3) showed that there were consistently more roots in the plots with fertiliser than in the control plots, although these differences were not usually significant at the 5% level. Root length of the <1 mm fraction in the treatment with fertiliser was nearly double that of the control, for instance. Total root length was 73% greater in the treated plots ($p=0.0478$), and root weights followed similar trends. As the trees in these treatments differed only in foliar magnesium concentration and not in height or diameter (or, we therefore assume, above-ground biomass) these results indicate an improved root:shoot ratio in the treated trees. Observations of mycorrhizal activity associated with the root samples indicated mycorrhizal root tips were more abundant in the plots with fertiliser. These results suggest a better flow of carbon to the root system and an improvement in the amount of substrate available for the mycorrhizas.

TABLE 3–Effect of magnesium fertiliser on root length and biomass in the top 20 cm of soil in 7-year-old *P. radiata*, Kaingaroa Forest.

Treatment	Root diameter class (mm)							
	<1	1–2	>2	Total	<1	1–2	>2	Total
	L_v (cm/cm^3)				kg/ha			
Control	0.0855	0.0260	0.0086	0.1202	277.9	446.1	1063.4	1787.7
Mg	0.1533	0.0448	0.0103	0.2085	613.9	642.1	2195.2	3451.6
Source of variation	Probability > F							
Mg	0.0941	0.0707	0.6048	0.0487	0.0533	0.3949	0.2020	0.1731

Effect of Magnesium Deficiency on Root Growth and Root:Shoot Ratio, Tauhara

There was significantly greater (p=0.0289) root biomass in the <1 mm root fraction in plots treated with magnesium (Table 4), indicating a below-ground response to the fertiliser. However, when total root biomass was assessed it was concluded that while there was a trend towards increased root biomass in the treated plots this was not significant at the 5% level. Results of the ANOVA done on the root:shoot ratio showed there were no significant treatment effects or interactions, though both applying magnesium and removing grass competition caused the root:shoot ratio to increase. This indicated a trend towards improved below-ground allocation although at this stage it was not statistically significant.

The four treatment combinations had mean foliar magnesium concentrations ranging from 0.6 to 0.95 mg/g, indicating varying degrees of magnesium deficiency. Regression analysis of plot mean foliar magnesium concentrations *v.* root:shoot ratio was not significant ($r^2 = 0.0018$, p>F 0.8912). It appears, therefore, that in this instance the dry matter allocation pattern was not related to degree of magnesium deficiency. Similarly, no relationship was found between the number of mycorrhizal root tips and magnesium treatment or degree of deficiency, although there was an indication that grass cover decreased the number of mycorrhizal root tips.

TABLE 4–ANOVA results of treatment effects on root growth, root : shoot ratio, foliar magnesium concentrations and number of mycorrhizal root tips in 3-year-old *P. radiata*, Tauhara Forest.

Treatment	Root biomass (kg/ha) by diameter class (mm)					Root: shoot ratio	Mycorrhizal tips/cm^3	Foliar Mg (mg/g)
	>5	2–5	1–2	<1	Total			
0 Mg	193.5	182.9	120.9	157.0	654.5	0.0583	0.478	0.61
400 kg Mg	126.7	273.3	204.4	314.3	918.8	0.1001	0.412	0.90
0 grass	288.1	356.9	226.9	343.9	1215.9	0.1095	0.511	0.73
100% grass	32.1	99.3	98.4	127.5	357.4	0.0488	0.379	0.78
Source of variation	Probability > F							
Mg	0.8317	0.4535	0.0938	0.0289	0.0588	0.2687	0.3075	0.0001
Grass	0.0115	0.0326	0.0204	0.0065	0.0022	0.1207	0.0585	0.2211
Mg * G	0.3678	0.3804	0.1040	0.0630	0.0529	0.3169	0.6140	0.3640

DISCUSSION

On sites with low plant-available magnesium levels it has been suggested that photosynthesis and carbon transformations in plants are adversely affected by a shortage of magnesium and this decreases allocation of carbon compounds to the root system (Marschner 1986; Ericsson 1991). This results in less-vigorous root growth and less mycorrhizal activity. The volume of soil exploited by the tree could therefore be less, so further reducing the amount of magnesium available to the tree. In turn, this would decrease carbon fixation and other processes requiring magnesium. This cycle could lead to a spiral of decline, until the tree reaches a new equilibrium with the site, at a slower growth rate. In severe cases trees could stagnate, as has been noted at a number of sites in Kaingaroa Forest (Hunter *et al.* 1986). Decreasing leaf area by pruning could place the trees under additional stress.

If a decline in root growth occurs due to magnesium deficiency, it should be possible to measure a change in allocation of photosynthate in plants on deficient sites. This was shown in the perlite medium experiment where total biomass production in seedlings with magnesium concentrations below Will's critical level of 1.0 mg/g and obvious deficiency symptoms (the 0.2 and 1.0 mg/ℓ treatments) decreased by between 60% and 80% (Table 1), and root:shoot ratio decreased by approximately 25%. As root:shoot ratios were the same for both the 0.2 mg/ℓ and 1.0 mg/ℓ treatments, it may be that there was an "on/off" mechanism occurring between 1.0 mg/ℓ and 10.0 mg/ℓ rather than a gradual decrease in rate of carbon fixation and transformations. With only three treatments, however, it was not possible to test this hypothesis. That the deficiency symptoms were caused primarily by a lack of magnesium was indicated by the very rapid growth improvements (within 1–2 weeks) that were recorded when magnesium sulphate was applied to the foliage in the 1.0 mg/ℓ treatment. The root:shoot ratio increased after foliar magnesium application (Table 2) indicating that the plants allocated proportionately more photosynthate to the roots even though the concentration of magnesium available in the perlite had not altered.

The magnesium-deficient 7-year-old trees at the Kaingaroa site showed large improvements in root biomass after fertiliser application (Table 3) and a doubling of fine root length. As there was no difference between treated and untreated plots in above-ground growth, as measured by height and diameter, this suggests an increased root:shoot ratio. The stimulation of roots by fertiliser could be a reason for the reported slow response of *P. radiata* to magnesium fertiliser, with the response below ground preceding an improvement in stem volume increment. In this situation trees apparently allocate photosynthate preferentially to the roots. In addition to the stimulation of the root system, mycorrhizal activity was greater in the treated plots, and this was probably due to an improvement in carbon availability to the fungi.

The results from the 3-year-old trees at the Tauhara site were less clear. While fine root biomass was increased by magnesium fertiliser, there was no relationship between fertiliser treatment and root:shoot ratio or number of mycorrhizal root tips. Foliar magnesium concentrations were marginal to deficient for about half of the plots but this was not reflected in a change in root:shoot ratio. However, none of the plots showed severe deficiency symptoms. The trees at Kaingaroa, by contrast, had been severely deficient since planting, and had had 6 years to rebuild their root systems after fertiliser application. Differences may therefore have had time to develop.

CONCLUSIONS

In this study magnesium deficiency affected dry matter allocation patterns in *P. radiata*, decreasing the root:shoot ratio. This was measured in seedlings under glasshouse conditions where a decrease in root:shoot ratio of 25% was recorded, and also in 7-year-old *P. radiata* at Kaingaroa Forest, where trees treated with magnesium had up to twice as much root length as deficient trees of the same size. The same effect was not detected in 3-year-old trees at the Tauhara site with foliar magnesium concentrations ranging from deficient to sufficient, although fine root biomass was increased. It may be that the changes are gradual and will develop with time at this site, or that the threshold, as suggested by the perlite experiment, had not yet been reached. Mycorrhizal activity, assessed subjectively at Kaingaroa, was higher in the treated plots, indicating a greater carbon pool for the fungi. However, when measured at Tauhara, no differences were found.

The changes in rooting density will have implications for magnesium uptake by the trees. Up to 50% less soil volume would be exploited by roots of the trees at Kaingaroa when they are suffering from a shortage of magnesium. This decreases the pool of magnesium and other nutrients available to the trees. The slow above-ground growth response noted in *P. radiata* after magnesium application may therefore be due to preferential allocation of dry matter below ground to rebuild a diminished root system.

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