ABOVE-GROUND DRY MATTER AND NUTRIENT CONTENT OF PINUS RADIATA AS AFFECTED BY LUPIN, FERTILISER, THINNING, AND STAND AGE

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ABSTRACT

Dry matter and nutrient content of above-ground tree components were estimated at ages 7, 10.5, and 17 years in stands of **Pinus radiata** D. Don established on a nitrogen-deficient sand dune. Experimental treatments included lupin (**Lupinus arboreus** Sims) exclusion and biennial fertiliser application in a replicated split-plot factorial design with stocking reductions as subplots.

Lupin and fertiliser treatments significantly increased growth, with the most productive stands accumulating twice as much dry matter and nutrients as the least productive. The distribution of dry matter and nitrogen between crown and stem changed with stand age and stocking but not with fertiliser addition. Lupin stimulated crown development more than the stem during early growth of the trees but this effect disappeared after the suppression of lupin by the pines. By age 7 years, the accumulated application of 570 kg fertiliser N/ha was less effective than lupin as a source of nitrogen. Relative to the controls, nitrogen accumulation in the above-ground tree components represented only 12% of added fertiliser in both thinned and unthinned stands. It appears that nitrogen not immediately available to the young trees was quickly leached from the sand. Application of a further 392 kg fertiliser N/ha between ages 7 and 10 gave an increase in above-ground tree dry matter and nitrogen content. More significantly, on this naturally nitrogen-deficient site, growth of stands with fertiliser surpassed those with lupin. Lupin was suppressed by the pines at stand age 5 and fertiliser application ceased at age 10. Efficiency of nitrogen accumulation in above-ground tree components after fertiliser application was still only 12%, averaged across the thinning treatments. However, much of the nitrogen incorporated in the trees was evident as needle litter during this stage. The continued high growth rate at age 17 indicates that nitrogen mineralisation made this nitrogen available again. The tightness of the bio-geo-chemical cycle after canopy closure is likely to ensure that the benefits achieved by earlier nitrogen additions are maintained.

Keywords: biomass; drought; long-term growth; nitrogen-fixation; nitrogen-fertiliser; **Lupinus arboreus**; **Pinus radiata**.

INTRODUCTION

Woodhill Forest is a 9000-ha plantation of *Pinus radiata* established on coastal sands. Productivity is low by New Zealand standards. Factors known or suspected of

limiting productivity are nitrogen and moisture supplies; recently-formed sand dunes have only 0.008% N – mostly in unavailable forms (Gadgil 1983), and soil moisture content at field capacity is only 8% to 10% by volume (Jackson, Jackson & Gifford 1983). A long-term experiment was set up in 1968 to investigate the importance of these two factors.

Plantation establishment normally begins with planting of marram grass (*Ammophila arenaria* (L.) Link) to stabilise the bare sand, followed by sowing of lupin. Two years later the lupin is crushed and pine seedlings are planted. Immediate and prolific lupin regrowth occurs and at least one release cutting of the lupins is needed before the pines suppress them. The treatments, which followed the normal plantation establishment procedure outlined above, were initiated at the time of tree planting. Lupin regrowth was excluded and fertiliser was applied in a 2 × 2 factorial. These main treatments were overlain with thinning treatments.

Basal area and height development (Jackson, Gifford, & Graham 1983), soil moisture status (Jackson, Jackson, & Gifford 1983), nutrient pools and fluxes at stand age 14 years (Baker *et al.* in press), soil nitrogen availability, and foliar analysis (Gadgil *et al.* 1984; Madgwick *et al.* 1983) have already been reported. In summary, these reports found no significant main-treatment effects for the first 5 years of stand development, by which time the pines had suppressed the lupin. Thereafter the pattern of foliar nitrogen concentration, height and diameter development of the trees, and moisture status of the sand down to at least 4 m diverged markedly.

Gadgil *et al.* (1984) found that lupin-exclusion plots without fertiliser developed chronic nitrogen-deficiency symptoms after stand age 5 years when foliar nitrogen values in February dropped from 1.5%, initially, to 0.8%. Sufficient reserves of nitrogen had accumulated during the marram/lupin phase prior to tree planting to provide for the early nitrogen requirements of the trees but the reserves were apparently inadequate to meet the high demand for nitrogen known to occur at this age (Madgwick *et al.* 1977). In lupin plots without fertiliser, foliar nitrogen declined to around 1.1% in February within 2 years after pines suppressed the lupin. In the fertiliser treatment, foliar nitrogen levels declined to around 1.2% by age 7 in spite of applications of 56 kg fertiliser N/ha at 6-monthly intervals for the first 10 years after planting. Foliar-nitrogen levels beyond age 10 years, when fertiliser was discontinued, increased to 1.3% at age 12 and declined to 1.2% at age 17. Jackson, Gifford, & Graham (1983) found that the response to fertiliser and lupin was additive in terms of stand basal area development. Gadgil *et al.* (1984) suggested a low level of retention of fertiliser nitrogen in the mineral soil and percentage of nitrogen uptake by the trees. Baker *et al.* (in press) conjectured that all stands were nitrogen-deficient at stand age 14 years and would respond to fertiliser. By foliar analysis standards (Will 1985) the pines were deficient. However, while fertiliser was being applied at a rate known to be in excess of requirements, foliar nitrogen concentrations remained low, especially in relation to stem growth.

Soil moisture status was affected by nutritional treatments after stand age 7 years (Jackson, Jackson, & Gifford 1983). Plots without lupin or fertiliser showed depletion of soil moisture compared to unplanted sites but always remained above –5 bars, the

point at which diameter growth stops. In contrast, lupin regrowth and fertiliser-treated plots depleted soil moisture to below –5 bars throughout the profile during late summer and autumn. The 60–70% greater stem volume growth of fertiliser-treated over control plots suggested that nutritional factors over-rode the effects of seasonal moisture deficits. Jackson, Jackson, & Gifford (1983) suggested that the more productive stands withdrew water from below the maximum depths monitored.

After thinning, percentage of foliar nitrogen increased during the first year or two before returning to pre-thinning levels (R. L. Gadgil pers. comm.). Thinning also significantly raised soil moisture status, particularly in plots with high foliar nitrogen status, but this effect rapidly diminished after 2 years and was insignificant after 5 years.

It is well established that *P. radiata* productivity on coastal sands is markedly increased by the addition of nitrogen. Still unclear are the mechanisms underlying this response, the maximum productivity that could be achieved, and the consequences of nutrient removal through harvest.

We report a series of biomass and nutrient content determinations made for the experimentally treated plots. The specific objectives addressed were to:

- Examine stand structure to provide a better understanding of the process of canopy development associated with the stem response to treatment;
- Evaluate the effect of lupin- and fertiliser-derived nitrogen on foliage, branches, and stems, both with and without thinning;
- Discuss the roles of nitrogen and moisture supply as factors limiting above-ground nitrogen and dry matter accumulation in *P. radiata.*

MATERIALS AND METHODS

Site Description and Experimental Treatments

The experiment is located in Cpt 138 of Woodhill Forest (36° 45′ S, 174° 26′ E), on a large dune approximately 1.3 km inland. The area was planted with marram grass in June (winter) 1965, treated with "Nitromoncal" (granulated lime-ammonium nitrate mix) in November, and lupin was sown in April 1966. *Pinus radiata* seedlings were machine planted at 2.4 × 1.8 m spacing in June 1968. The Lowther planting machines crushed but did not kill the lupin.

The experiment was established immediately after tree planting and the prescribed treatments were maintained for 10 years. Main treatments, which each occupied an area of 0.566 ha, comprised a 2 × 2 factorial with and without lupin regrowth and with and without fertiliser, replicated twice in a randomised block design. In December 1968 plots in which no lupin regrowth was to be permitted were crushed and sprayed between the rows of trees with 2,4,5-T/2,4-D herbicides and thereafter were manually weeded. Hence, the control stands (with no lupin or fertiliser) were not permitted the further cycles of lupin growth immediately after planting and after heavy thinning characteristic of *P. radiata* stands at Woodhill. The marram/lupin understorey resurgence and development during the 5 years prior to suppression by the developing pines have been documented by Jackson, Gifford, & Graham (1983) and Gadgil *et al.* (1984). The

fertiliser regime was designed to supply an adequate and balanced supply of macronutrients to the pines. Amounts of elements applied included 962 kg N/ha, 407 kg P/ha, 412 kg K/ha, 138 kg S/ha, 294 kg Mg/ha, and 203 kg Ca/ha. These were supplied in biennial applications of different types of fertiliser over a 10-year period as reported by Gadgil *et al.* (1984).

Thinning treatments were imposed in a split plot design within each of the main plots. Subplots were maintained at the initial stocking of 2224 stems/ha throughout, or thinned to 1483 stems/ha at age 2, or thinned to 741 stems/ha at age 4, or thinned to 1483 stems/ha at age 4 followed by a further reduction to 371 stems/ha at age 8. All plots were low pruned to 2 m height in 1975. The criterion for scheduling thinning operations given by Jackson, Gifford, & Graham (1983) prevented undue loss in crop-tree diameter growth resulting from inter-tree competition.

Assessment plots each of 0.0405 ha provided basic mensurational data on stand height and basal area development (Jackson, Gifford, & Graham 1983), foliar analysis and soil data (Gadgil *et al.* 1984), and atmospheric inputs, nutrient cycling, and nutrient pools at stand age 14 years (Baker *et al.* in press).

Biomass Determination

Biomass was measured on three trees per subplot sampled from February through May as follows. All subplots were sampled in 1975. One block (excluding subplots at 371 stems/ha) was sampled in 1978, the other in 1979 because of time constraints. No data were collected from stands thinned to 371 stems/ha as biomass sampling at this stocking would unduly affect the growth of residual trees. Unthinned subplots were sampled in 1985. Hence, 96, 36, 36, and 24 trees were harvested in 1975, 1978, 1979, and 1985, respectively. Trees were selected at random from the subplot surround, except in 1985 when plot trees were sampled.

Each tree was felled at 10 cm above ground-level, and measured for total height and dbh. Height to and stem diameter 10 cm below each branch cluster (whorl) were measured. Diameter of each branch was measured at 2.5 cm from the stem. All cones were collected. Dead branch clusters at the base of the live crown were weighed fresh, the branches were cut into sections, and a subsample of known fresh weight was taken. The green crown was divided into four height zones of equal length. One random branch was taken from each zone and weighed fresh, measured for total length, and divided into components (fascicles by age-class, wood, bark, dead twigs; except in 1985 when the latter three components were not separated). The stem was divided into four sections of equal length and weighed fresh. Sample discs were cut and weighed fresh before being divided into wood and bark. All samples were dried to constant weight at 65°C in forced-ventilation ovens.

Subplot biomass was calculated from the sample data using ratio methods. The live branch data from the three sample trees per subplot were combined by zone, and ratios between component weight and branch cross-sectional area calculated. These ratios were applied to the branch census data of individual trees to give estimates of fascicle (by age) and branch weight by height zone. The weights of the four zones were summed to give tree weights. In 1975, separate estimates were derived to represent

pre- and post-pruning results. Stemwood, bark, and dead branch cluster dry weights were obtained by multiplying total fresh weight by the dry matter fraction in the sample. Subplot biomass was estimated using the basal area ratio method (Madgwick 1981).

Nutrient Analysis

Nutrient analyses, expressed on an oven-dry weight basis, were made on composite samples of each component of each tree. Sample material was combined in proportion to its contribution to the total tree oven-dry weight, except for foliar nitrogen in 1975 which was determined by height zone (Madgwick *et al.* 1983). Nitrogen was determined colorimetrically after Kjeldahl digestion. Other elements were measured after nitric/perchloric acid digestion. Phosphorus and boron were determined colorimetrically; sulphur turbidimetrically; potassium, calcium, and sodium by flame emission; and magnesium, iron, manganese, zinc, and copper by atomic absorption (Analytical Services Ltd).

The following data are unavailable. Pruned branch matter was not separately analysed for nutrients, so post-pruning results in 1975 (age 7) are available only in terms of dry matter. Dead branches from Block 1 were not sampled for dry weight or nutrients in 1975. Cones were not analysed for nutrients in 1975. Fascicle weights exclude those attached directly to the stem as stem fascicles were not expected to exceed 5% of the total fascicle dry matter and nutrient content.

Statistical Analysis

Estimates of plot dry matter and nutrients were statistically independent but, because the sampling scheme was not balanced, a full split-plot analysis was not possible. The samplings in 1978 and 1979 were combined and designated as age 10.5 years replications. Data from a given stocking were combined over all sampling dates to investigate changes in response over time. Data for each year were analysed for nutrition and stocking effects.

ANOVAs were performed using Genstat (Lawes Agricultural Trust 1980). In some analyses data transformation was necessary to meet statistical assumptions.

RESULTS

Stocking, lupin, fertiliser, and sampling date all affected the dry weight, tissue nitrogen concentration, and nitrogen content of most stand components. Treatment means are presented in Tables 1–12, with significant between-year effects at the right of the tabulated data and within-year effects at the foot of each table. Treatment interactions indicate that the nature of the responses to nutritional treatments was contingent on thinning and varied with time. These interactions resulted inevitably in some overlap between the section headings listed below.

Age Effects

The canopy was closed at the age 7 biomass assessment in unthinned stands and stands thinned to 1483 stems/ha, but closure did not occur until age 10.5 years in stands thinned to 741 stems/ha. Hence, thinning significantly reduced both 0- to

TABLE 1—Fascicle dry matter (t/ha) as influenced by nutrition, thinning, and stand age

	0- to 1-year fascicles					Total fascicles				
	Stand age (years)				Between-year	Stand age (years)				Between-year
	7	7P	10.5	17	effects	7	7P	10.5	17	effects
2224 stems/ha										
Control	3.6	3.2	2.9	2.8	Y?	8.5	5.9	6.2	5.6	F*
Lupin	6.3	5.5	3.6	3.6	F**	14.2	9.3	8.6	9.9	L**
Fertiliser	5.6	5.4	5.2	5.1	L*	9.7	8.5	10.4	9.0	
Lupin + fert.	6.4	5.4	6.4	5.7		13.1	9.5	12.7	10.8	
1483 stems/ha										
Control	3.3	3.0	2.8	-	F?	7.6	4.4	6.1	-	F*
Lupin	5.5	3.5	4.3	-		12.3	5.7	10.3	-	L*
Fertiliser	4.5	3.6	6.2	-		8.6	5.3	13.0	-	YxF?
Lupin + fert.	6.3	4.8	4.7	-		12.0	7.8	10.4	-	YxL?
										FxL*
741 stems/ha										
Control	2.5	1.9	2.9	-	F?	6.1	3.4	6.2	-	L?
Lupin	4.8	3.3	3.5	-	L*	8.9	5.2	7.2	-	
Fertiliser	4.0	3.4	4.6	-		8.2	5.4	9.7	-	
Lupin + fert.	5.0	4.1	7.1	-		9.7	6.3	13.6	-	
Within-year effects	L?	na	F*			L*	na	F*		
	S*					S***				
						LxS*				

Explanation of abbreviations and notation for all Tables:

P	=	Stands pruned	na	=	Not included in statistical analysis
Y	=	Year	?	=	Significant at $p < 0.10$
F	=	Fertiliser	*	=	Significant at $p < 0.05$
L	=	Lupin	**	=	Significant at $p < 0.01$
S	=	Stocking	***	=	Significant at $p < 0.001$

TABLE 2—Branch dry matter (t/ha) as influenced by nutrition, thinning, and stand age

	Live branches					Dead branches				
	Stand age (years)				Between-year	Stand age (years)				Between-year
	7	7P	10.5	17	effects	7	7P	10.5	17	effects
2224 stems/ha										
Control	10.1	5.4	9.1	6.9	Y*	1.2	0.0	2.6	8.9	na
Lupin	13.9	8.6	11.1	13.0	F*	1.4	0.0	1.8	12.0	
Fertiliser	10.0	7.1	12.2	16.0	L*	1.9	0.0	4.7	16.3	
Lupin + fert.	16.3	9.4	16.8	18.4		2.7	0.0	3.8	20.1	
1483 stems/ha										
Control	7.6	3.4	8.9	-	F*	0.1	0.0	1.1	-	na
Lupin	11.3	4.9	10.3	-		0.1	0.0	0.5	-	
Fertiliser	13.3	7.5	13.7	-		1.4	0.0	2.1	-	
Lupin + fert.	16.0	8.9	11.0	-		1.0	0.0	1.7	-	
741 stems/ha										
Control	9.4	5.0	7.3	-	F*	0.2	0.0	0.5	-	na
Lupin	11.4	6.2	9.1	-	YxF?	0.2	0.0	0.2	-	
Fertiliser	12.0	7.2	15.3	-		0.3	0.0	1.7	-	
Lupin + fert.	10.3	6.6	20.7	-		0.1	0.0	0.2	-	
Within-year effects		na	F? FxS?	F?		na	na	S**	F?	

TABLE 3—Stem dry matter (t/ha) as influenced by nutrition, thinning, and stand age

	Stem wood				Stem bark			
	Stand age (years)			Between-year effects	Stand age (years)			Between-year effects
	7	10.5	17		7	10.5	17	
2224 stems/ha								
Control	26.9	56.5	97.1	Y**	3.5	8.0	20.0	Y**
Lupin	29.7	68.2	142.5	F**	3.7	8.5	23.2	F**
Fertiliser	31.9	74.9	162.4	L*	3.7	8.7	26.9	L?
Lupin + fert.	30.4	88.9	185.8	YxF** YxL?	4.1	10.2	30.4	YxF*
1483 stems/ha								
Control	22.5	47.5	-	F?	2.9	5.6	-	Y*
Lupin	20.5	52.5	-		2.6	6.2	-	
Fertiliser	23.9	78.0	-		3.3	7.2	-	
Lupin + fert.	26.6	66.9	-		3.3	7.8	-	
741 stems/ha								
Control	16.2	34.7	-	Y?	2.0	4.1	-	Y*
Lupin	15.1	40.4	-	F***	2.0	4.7	-	F*
Fertiliser	20.9	58.1	-	YxF*	2.6	5.4	-	
Lupin + fert.	18.5	53.6	-		2.4	5.7	-	
Within-year effects	S***	F* S***	F* L?		S***	S***	F?	

TABLE 4—Cone dry matter (t/ha) as influenced by nutrition, thinning, and stand age

	Stand age (years)			Between-year effects
	7	10.5	17	
2224 stems/ha				
Control	0.58	1.64	4.86	Y*
Lupin	0.22	0.92	7.10	
Fertiliser	0.47	2.01	7.17	
Lupin + fert.	0.07	1.76	5.62	
1483 stems/ha				
Control	0.33	1.41	-	Y*
Lupin	0.25	1.01	-	L*
Fertiliser	0.56	2.17	-	
Lupin + fert.	0.03	0.74	-	
741 stems/ha				
Control	0.33	0.96	-	
Lupin	0.11	1.17	-	
Fertiliser	0.19	2.31	-	
Lupin + fert.	0.02	1.21	-	
Within-year effects	L*	F** L** FxL*		

TABLE 5—Fascicle nitrogen concentrations (%) as influenced by nutrition, thinning, and stand age

	0- to 1-year fascicles				1- to 2-year fascicles			
	Stand age (years)			Between-year effects	Stand age (years)			Between-year effects
	7	10.5	17		7	10.5	17	
2224 stems/ha								
Control	1.06	0.89	0.77	F**	0.82	0.84	0.69	Y?
Lupin	1.16	0.97	1.07	L*	0.88	0.94	0.90	F***
Fertiliser	1.27	1.09	1.02		0.99	1.01	0.96	L**
Lupin + fert.	1.23	1.19	1.14		1.08	1.14	1.01	
1483 stems/ha								
Control	0.98	0.92	-	F**	0.81	0.90	-	F***
Lupin	1.13	0.95	-		1.01	0.88	-	L?
Fertiliser	1.28	1.12	-		1.02	0.99	-	YxL**
Lupin + fert.	1.31	1.11	-		1.03	0.96	-	FxL*
								YxFxL*
741 stems/ha								
Control	1.14	0.89	-	F***	0.91	0.85	-	F**
Lupin	1.21	0.97	-	L?	1.01	0.94	-	
Fertiliser	1.30	1.15	-	YxF?	1.07	1.05	-	
Lupin + fert.	1.32	1.23	-		1.06	1.12		
Within-year effects	F*	F**	L?		F*	F**	F*	
		L?			L?	L?	L?	
					S?	S*		
						FxS*		
						LxS*		

TABLE 6—Fascicle and cone nitrogen concentrations (%) as influenced by nutrition, thinning, and stand age

	2- to 3-year fascicles				Cones			
	Stand age (years)			Between-year effects	Stand age (years)			Between-year effects
	7	10.5	17		7	10.5	17	
2224 stems/ha								
Control	0.77	0.78	0.65	F***	-	0.22	0.43	na
Lupin	0.77	0.82	0.84	L*	-	0.33	0.48	
Fertiliser	0.88	0.91	0.84		-	0.32	0.51	
Lupin + fert.	0.94	0.90	0.93		-	0.35	0.47	
1483 stems/ha								
Control	0.78	0.80	-		-	0.34	-	na
Lupin	0.85	0.81	-		-	0.54	-	
Fertiliser	0.86	0.91	-		-	0.36	-	
Lupin + fert.	0.88	0.86	-		-	0.35	-	
741 stems/ha								
Control	0.85	0.75	-	YxL*	-	0.27	-	na
Lupin	0.85	0.81	-		-	0.41	-	
Fertiliser	0.95	0.79	-		-	0.41	-	
Lupin + fert.	0.83	0.94	-		-	0.32	-	
Within-year effects	F*		F**		na	S?		
			L**					
			FxL?					

TABLE 7—Branch nitrogen concentrations (%) as influenced by nutrition, thinning, and stand age

	Live branches				Dead branches			
	Stand age (years)			Between-year effects	Stand age (years)			Between-year effects
	7	10.5	17		7	10.5	17	
2224 stems/ha								
Control	0.24	0.20	0.18	F?	-	0.10	0.10	na
Lupin	0.38	0.21	0.24		-	0.15	0.11	
Fertiliser	0.43	0.26	0.24		-	0.12	0.11	
Lupin + fert.	0.45	0.21	0.25		-	0.09	0.12	
1483 stems/ha								
Control	0.30	0.22	-		-	0.14	-	na
Lupin	0.33	0.21	-		-	0.12	-	
Fertiliser	0.37	0.26	-		-	0.09	-	
Lupin + fert.	0.32	0.22	-		-	0.10		
741 stems/ha								
Control	0.22	0.19	-	Y?	-	0.21	-	na
Lupin	0.28	0.23	-	F**	-	0.12	-	
Fertiliser	0.36	0.25	-	YxF*	-	0.16	-	
Lupin + fert.	0.36	0.22	-	FxL?	-	0.10	-	
Within-year effects	F?				na			

TABLE 8—Stem nitrogen concentrations (%) as influenced by nutrition, thinning, and stand age

	Stem wood				Stem bark			
	Stand age (years)			Between-year effects	Stand age (years)			Between-year effects
	7	10.5	17		7	10.5	17	
2224 stems/ha								
Control	0.07	0.07	0.03	Y**	0.29	0.19	0.11	Y**
Lupin	0.09	0.06	0.04	F*	0.36	0.31	0.16	F***
Fertiliser	0.08	0.06	0.04	L*	0.42	0.32	0.17	L***
Lupin + fert.	0.13	0.08	0.04	YxL? FxL?	0.47	0.37	0.20	
1483 stems/ha								
Control	0.07	0.05	-	F*	0.32	0.23	-	Y?
Lupin	0.10	0.05	-	L*	0.43	0.30	-	F*
Fertiliser	0.09	0.06	-	FxL*	0.43	0.36	-	FxL*
Lupin + fert.	0.09	0.07	-		0.39	0.34	-	
741 stems/ha								
Control	0.06	0.06	-	Y*	0.33	0.23	-	L*
Lupin	0.10	0.06	-	F*	0.39	0.26	-	
Fertiliser	0.09	0.07	-	L*	0.37	0.34	-	
Lupin + fert.	0.11	0.08	-		0.41	0.37	-	
Within-year effects	F* L** FxL? FxLxS*				F* L*	F*	F* L?	

TABLE 9—Fascicle nitrogen content (kg/ha) as influenced by nutrition, thinning, and stand age

	0- to 1-year fascicles				Total fascicles			
	Stand age (years)			Between-year effects	Stand age (years)			Between-year effects
	7	10.5	17		7	10.5	17	
2224 stems/ha								
Control	37.4	25.4	22.0	Y*	77.5	52.8	39.6	Y*
Lupin	73.8	35.0	37.9	F***	141.9	79.0	85.2	F**
Fertiliser	70.7	57.2	52.8	L**	111.9	106.7	88.3	L**
Lupin + fert.	78.5	76.2	65.3		150.5	141.0	112.4	
1483 stems/ha								
Control	31.1	25.1	-	F*	65.5	52.8	-	F**
Lupin	62.9	40.4	-	YxL?	129.8	91.6	-	L*
Fertiliser	57.5	69.8	-		98.7	135.9	-	YxL*
Lupin + fert.	82.0	51.7	-		140.4	105.3	-	FxL*
741 stems/ha								
Control	28.4	26.0	-	F*	59.8	51.1	-	Y*
Lupin	57.8	34.0	-	L*	98.3	67.6	-	F*
Fertiliser	52.8	53.4	-		96.6	103.2	-	L?
Lupin + fert.	66.2	87.5	-		109.8	158.7	-	
Within-year effects	L? S?	F** L?			L* S**	F** L?		

TABLE 10—Branch nitrogen content (kg/ha) as influenced by nutrition, thinning, and stand age

	Live branches				Dead branches			
	Stand age (years)			Between-year effects	Stand age (years)			Between-year effects
	7	10.5	17		7	10.5	17	
2224 stems/ha								
Control	24.2	18.0	12.6	Y?	-	2.82	8.9	na
Lupin	52.2	23.0	30.8	F**	-	2.77	13.2	
Fertiliser	42.7	32.8	37.3	L*	-	5.51	17.7	
Lupin + fert.	73.8	28.3	44.5	YxL?	-	6.18	24.1	
1483 stems/ha								
Control	21.5	19.0	-	F*	-	1.68	-	na
Lupin	36.8	21.3	-		-	0.46	-	
Fertiliser	51.5	34.3	-		-	1.91	-	
Lupin + fert.	49.8	23.0	-		-	1.59	-	
741 stems/ha								
Control	19.8	13.6	-	F*	-	0.98	-	na
Lupin	31.3	20.6	-		-	0.34	-	
Fertiliser	45.0	37.6	-		-	2.94	-	
Lupin + fert.	37.1	44.3	-		-	0.19	-	
Within-year effects	S* LxS*	F* S? FxS? LxS?	F*		na	S*** FxS?	F*	

TABLE 11—Stem nitrogen content (kg/ha) as influenced by nutrition, thinning, and stand age

	Stem wood				Stem bark			
	Stand age (years)			Between-year effects	Stand age (years)			Between-year effects
	7	10.5	17		7	10.5	17	
2224 stems/ha								
Control	18.8	42.1	33.0	Y*	10.2	15.7	21.9	Y*
Lupin	26.4	39.8	57.6	F**	13.7	26.2	37.1	F***
Fertiliser	27.3	45.0	63.5	L**	15.6	26.8	44.4	L***
Lupin + fert.	38.1	71.6	80.2		19.2	37.1	60.7	YxF* YxL?
1483 stems/ha								
Control	17.2	23.7	-	F*	9.2	13.3	-	F*
Lupin	20.5	28.5	-		11.0	18.6	-	
Fertiliser	22.9	51.7	-		14.2	25.8	-	
Lupin + fert.	24.0	46.8	-		12.9	26.3	-	
741 stems/ha								
Control	10.5	20.7	-	F**	6.6	9.5	-	F***
Lupin	15.1	24.2	-	YxF*	7.7	12.2	-	L?
Fertiliser	18.6	38.1	-		9.4	18.5	-	YxF**
Lupin + fert.	19.4	42.9	-		9.9	20.8	-	
Within-year effects	F? S***	F? S*** FxLxS*	F* L?		F* S***	F** L* S*** LxS?	F* L?	

TABLE 12—Cone nitrogen content (kg/ha) as influenced by nutrition, thinning, and stand age

	Stand age (years)			Between-year effects
	7	10.5	17	
2224 stems/ha				
Control	-	3.8	21.5	na
Lupin	-	3.1	33.1	
Fertiliser	-	6.6	38.1	
Lupin + fert.	-	7.0	27.2	
1483 stems/ha				
Control	-	4.8	-	na
Lupin	-	5.4	-	
Fertiliser	-	7.2	-	
Lupin + fert.	-	2.6	-	
741 stems/ha				
Control	-	2.1	-	na
Lupin	-	5.0	-	
Fertiliser	-	13.0	-	
Lupn + fert.	-	6.7	-	
Within-year effects	na			

1-year and total fascicle weights at age 7 but not at age 10.5 (Table 1). Fascicle dry weights, nitrogen concentrations, and nitrogen contents of unthinned stands decreased with increasing stand age but this decline attained statistical significance only for fascicle nitrogen contents (Tables 1, 5, 6, 9).

Pruning at age 7 removed about 40% of the live branch weights (Table 2). These attained pre-pruning values by age 10.5 and increased further by age 17 in all but control stands. Thinning had little effect on live branch weights, with any real effects masked by sampling variability. Thinning significantly reduced branch nitrogen content (Table 10). Dead branches, which were confined mostly to dead branch clusters at the base of the crown, were higher in unthinned stands (Table 2).

Stem wood and bark dry weights increased but nitrogen concentrations decreased with age (Tables 3 and 8). The effect of these opposite trends on stem nitrogen content depended on the nutritional treatment (Table 11), with stem wood-plus-bark nitrogen content after age 10.5 unaffected by stand age in control stands but increasing in the more productive stands.

Cone weight increased with age (Table 4). Nitrogen concentrations and contents in cones in the unthinned plots increased from age 10.5 to 17 (Tables 6 and 12).

Crown dry matter and nitrogen contents, expressed as a percentage of above-ground tree weights, decreased as stands aged but increased with thinning (Table 13).

Lupin Effects

Lupin significantly increased 0- to 1-year and total fascicle dry weight (Table 1), fascicle N content (Table 9), stem wood and bark nitrogen concentrations (Table 8), and the ratio of crown to stem weight (Table 13) at age 7. These effects decreased with time. Only stem bark nitrogen content was increased by lupin at age 10.5 (Table 11). Lupin decreased cone weights at ages 7 and 10.5 (Table 4). Above-ground nitrogen content of stands with lupin decreased from stand age 7 to 10.5.

A partial recovery of lupin effects occurred by age 17. Above-ground nitrogen content increased (Fig. 1), as did stem wood weight in unthinned stands when analysed over time (Table 3), because it seems of the age 17 data. Increases in fascicle nitrogen concentrations (Tables 5 and 6) and stem wood and bark nitrogen contents (Table 11) provide further evidence of a partial recovery.

At age 7, thinning reduced the early effects of lupin on total fascicle weight (Table 1) as indicated by the L × S interaction; unthinned stands with lupin carried 67% more weight than controls, but in heavily thinned stands the difference was only 46%. Furthermore, stem wood nitrogen concentrations increased additively only in unthinned stands (F × L × S interaction in Table 8), while at age 10.5 stem wood nitrogen content increased additively in thinned but synergistically in unthinned stands (Table 11).

The proportion of fascicles in different age-classes was unaffected by treatment at age 7 but the ratio of 0–1 year to total fascicles decreased at age 17 in stands with lupin.

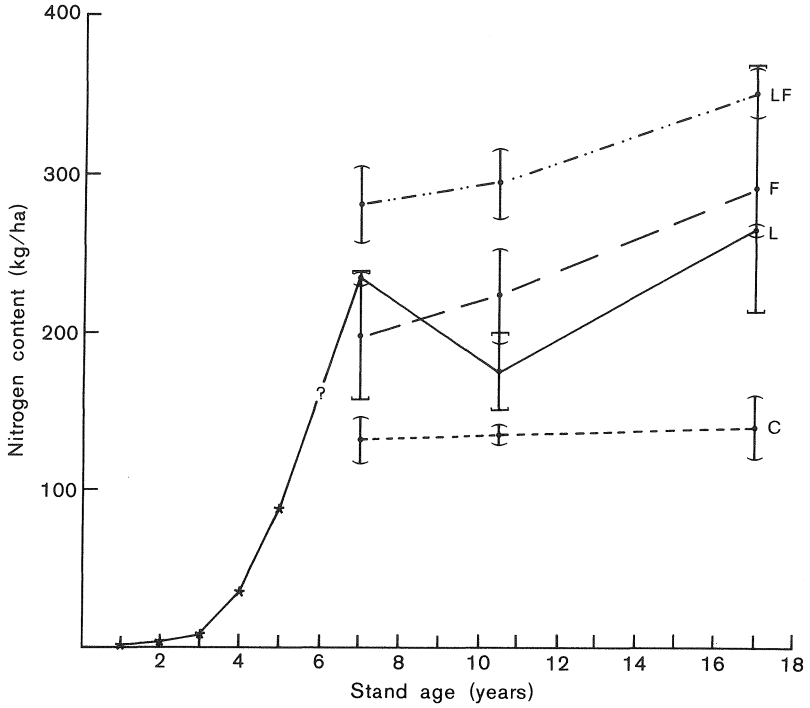

FIG. 1—Nitrogen accumulation in above-ground tree components of unthinned **Pinus radiata** plots without lupin or fertiliser (C), or with lupin only (L), fertiliser only (F), or lupin plus fertiliser (LF). Vertical bars represent the standard error of the mean of two subplots in each treatment (age 1- to 5-year data from Gadgil 1979).

Fertiliser Effects

Fertiliser additions did not significantly increase component weights or nitrogen content (except stem bark) at age 7 though nitrogen concentrations were significantly increased (Tables 11, 5, 6, and 8, respectively). At age 10.5 component dry weights, nitrogen concentrations, and nitrogen contents were almost all higher in fertilised stands, with most weight increases being statistically significant. Increases due to fertiliser appeared to persist at age 17, but few statistically significant differences persisted even though weights were often more than double those of the controls.

Fertiliser increased crown and stem component weights and nitrogen contents commensurately. Hence, the percentage of crown in the stand was not affected by fertiliser (Table 13). However, the percentage of 0–1 year to total fascicles at age 17 increased in stands with fertiliser (Table 14).

Significant interactions between fertiliser and either lupin or spacing were rare. Cones were an exception (Table 4).

TABLE 13—Crown dry matter and nitrogen content as a percentage of above-ground weight, as influenced by nutrition, thinning, and stand age

	Dry matter				Nitrogen			
	Stand age (years)			Between-year effects	Stand age (years)			Between-year effects
	7	10.5	17		7	10.5	17	
2224 stems/ha								
Control	38	19	10	Y***	78	55	48	Y**
Lupin	46	20	12	L*	83	60	55	
Fertiliser	36	22	11	YxL?	78	66	52	
Lupin + fert.	46	21	12		79	61	53	
1483 stems/ha								
Control	38	22	-	Y*	77	66	-	Y*
Lupin	50	26	-	L?	84	71	-	
Fertiliser	45	25	-		80	70	-	
Lupin + fert.	48	23	-		84	64	-	
741 stems/ha								
Control	45	26	-	Y*	82	68	-	Y?
Lupin	54	28	-	L*	85	72	-	L?
Fertiliser	45	28	-		82	71	-	
Lupin + fert.	48	36	-		83	76	-	
Within-year effects	L*	S***			L?	S***		
	S*	LxS?				FxS?		
						LxS?		

TABLE 14—Proportion of total fascicles aged 0-1 years old as influenced by nutrition, thinning, and stand age

	Stand age (years)		
	7	10.5	17
2224 stems/ha			
Control	41	47	49
Lupin	45	43	36
Fertiliser	57	50	57
Lupin + fert.	49	50	53
1483 stems/ha			
Control	41	46	-
Lupin	44	41	-
Fertiliser	52	48	-
Lupin + fert.	52	45	-
741 stems/ha			
Control	42	49	-
Lupin	54	48	-
Fertiliser	49	48	-
Lupin + fert.	55	52	-
Within-years effects			F*
			L*

Nutrient Accumulation Above Ground

Totals of above-ground dry matter and nutrient contents (Table 15) were highly intercorrelated and will be described for nitrogen in detail. Fertiliser and lupin increased the above-ground nitrogen content of the treated stands over control levels, though relative increases varied with time and stocking and were always small in efficiency terms (Table 16). The time-course of nitrogen accumulation for unthinned stands is illustrated in Fig. 1, including the earlier data of Gadgil (1979). The benefit of lupin at age 7 was most apparent, exceeding the gains due to fertiliser alone, but the rankings reversed by age 10.5. This reversal had already occurred at age 7 in stands thinned to 741 stems/ha (Table 16). At age 17 years the unthinned control stands had around 140 kg N/ha, half that in the stands with lupin or fertiliser (265 and 290 kg/ha, respectively). Stands with lupin plus fertiliser accumulated 350 kg N/ha, suggesting a less-than-additive response.

DISCUSSION

Role of Nitrogen

Tree requirements for nitrogen change with age and as a result of silviculture. High requirements are associated with canopy expansion in young stands or after thinning, but under closed canopy conditions demands are lower (Madgwick *et al.* 1977; Miller 1981). Many tree-growth responses to nitrogen have been reported both in terms of increased weights of foliage, branches, and stems per hectare (Miller & Miller 1976; Linder & Axelsson 1982; Brix 1983; Mead *et al.* 1984; Cromer, Barr, Williams, & McNaught 1985), and in terms of increased tissue-nitrogen concentrations (Cromer, Barr, & Tompkins 1985). Nambiar & Cellier (1985) suggested the need for caution when evaluating responses to fertiliser treatments, particularly in soil with high organic matter content; the latter does not apply to first-rotation *P. radiata* stands established on sand-dunes at Woodhill. Gadgil *et al.* (1984) concluded that all nutrients except nitrogen and possibly copper were available in adequate amounts based on foliar analysis. The interpretation of the responses to treatment reported here assumes nitrogen was the limiting nutrient.

The effects of improved nitrogen nutrition on tree nitrogen content were reflected initially by differences in tissue nitrogen concentration but later by differences in stand dry matter content. Nitrogen concentration in woody tissues is negatively correlated with size (Madgwick 1985) possibly because of nitrogen remobilisation from sapwood prior to heartwood formation (Orman & Will 1960). Our results suggest that nitrogen remobilisation may proceed to a common lower asymptote in the heartwood irrespective of nutritional treatment. Fertiliser doubled dry matter content on a per hectare basis. The lupin plus fertiliser treatment in this experiment raised fascicle weights to levels closely comparable to those found in closed canopy *P. radiata* stands on highly productive sites (Madgwick *et al.* 1977). The latter stands do not respond to nitrogen fertiliser unless they are concurrently thinned (Woollons & Will 1975), and provide the upper limit of fascicle weight/stand age relationships based on a synthesis of *P. radiata* biomass data (Madgwick 1985).

TABLE 15—Dry matter (t/ha) and nutrient (kg/ha) content of above-ground tree components, as influenced by nutrition, thinning, and stand age

	2224 stems/ha Stand age (years)			1483 stems/ha Stand age (years)		741 stems/ha Stand age (years)	
	7	10.5	17	7	10.5	7	10.5
Control							
DM	50.1	84.0	143.4	41.0	70.6	34.1	53.6
N	130.9	135.5	139.0	113.5	115.8	96.7	98.3
P	25.6	26.4	30.0	21.6	26.9	19.0	21.5
K	148.5	150.8	159.2	104.2	131.7	103.7	106.4
S	16.5	25.4	-	14.4	28.7	12.3	19.1
Ca	69.2	84.1	190.1	72.3	80.3	53.4	62.8
Mg	40.3	43.9	68.2	36.3	39.3	27.0	32.1
Na	22.2	32.4	-	21.0	27.4	21.0	23.7
Fe	2.25	3.08	-	1.59	2.74	1.52	2.30
Mn	3.81	3.24	4.93	3.50	3.07	2.93	2.79
Zn	0.85	1.13	2.03	0.76	0.94	0.61	1.02
Cu	0.13	0.12	0.13	0.17	0.16	0.14	0.10
B	0.41	0.54	-	0.31	0.51	0.31	0.47
Lupin							
DM	62.5	99.1	207.6	47.0	80.8	37.5	62.8
N	234.1	174.6	264.6	198.2	166.4	152.6	129.9
P	38.5	36.8	55.5	30.6	35.5	27.0	24.8
K	229.4	216.8	284.9	175.0	168.0	132.3	119.2
S	23.7	38.4	-	19.3	29.3	15.7	21.8
Ca	104.6	83.1	226.9	96.2	87.5	73.4	66.5
Mg	58.9	55.4	91.8	46.9	53.4	36.7	37.1
Na	28.9	45.0	-	30.3	32.8	18.9	27.1
Fe	3.40	3.40	-	2.01	2.48	1.72	1.96
Mn	4.62	3.97	8.93	4.63	3.68	2.95	2.20
Zn	1.15	1.37	2.54	1.03	1.29	0.78	0.90
Cu	0.19	0.20	0.20	0.17	0.14	0.18	0.15
B	0.54	0.71	-	0.44	0.72	0.33	0.42
Fertiliser							
DM	56.5	112.9	237.6	50.4	116.3	44.0	92.5
N	197.6	223.4	290.6	187.4	257.2	169.6	213.9
P	35.6	47.3	58.7	30.6	47.9	30.2	42.0
K	176.8	227.9	283.3	177.8	229.7	146.1	195.7
S	19.7	49.0	-	20.4	53.5	19.3	44.3
Ca	80.6	134.2	229.2	82.1	91.2	80.8	90.3
Mg	48.3	70.9	106.5	43.5	70.2	40.1	56.7
Na	28.3	59.1	-	31.5	57.7	23.7	40.5
Fe	2.19	4.92	-	2.62	3.33	2.21	2.98
Mn	4.05	4.40	10.0	3.11	3.04	3.38	2.96
Zn	0.78	1.46	2.76	0.70	1.41	0.73	1.23
Cu	0.14	0.33	0.26	0.13	0.34	0.11	0.24
B	0.44	0.93	-	0.36	0.85	0.33	0.66
Lupin + fert.							
DM	65.4	134.1	270.5	58.5	98.6	40.4	95.0
N	281.6	293.5	351.8	227.2	206.4	176.3	273.6
P	42.1	58.8	72.2	36.6	40.7	27.4	51.2
K	248.2	281.0	403.6	195.1	213.4	157.8	241.8
S	25.3	60.7	-	24.7	40.7	18.0	47.2
Ca	112.4	135.1	284.4	94.7	100.4	73.2	94.5
Mg	68.4	92.7	130.3	59.7	64.4	42.3	71.1
Na	34.1	57.3	-	30.9	46.9	29.5	56.6
Fe	2.67	4.08	-	2.58	3.24	1.70	3.38
Mn	2.82	3.75	10.3	2.93	2.54	1.90	2.72
Zn	0.87	1.69	2.72	0.81	0.99	0.58	1.28
Cu	0.15	0.21	0.28	0.15	0.23	0.09	0.22
B	0.62	1.44	-	0.44	1.01	0.34	0.87

TABLE 16—Contribution of lupin, fertiliser, and lupin plus fertiliser to the above-ground tree nitrogen content as influenced by thinning and stand age. Amounts are kilograms of nitrogen per hectare in excess of control stands. Percentage recovery of added nitrogen, in parentheses, assumes 400 kg N/ha fixation within 5 years in stands containing lupin; 570 and 962 kg fertiliser N/ha were applied by ages 7 and 10.5, respectively

	Stand age (years)		
	7	10.5	17
2224 stems/ha			
Lupin	103 (26)	39 (10)	126 (32)
Fertiliser	67 (12)	88 (9)	152 (16)
Lupin + fert.	151 (16)	158 (12)	213 (16)
1483 stems/ha			
Lupin	85 (21)	51 (13)	-
Fertiliser	74 (13)	141 (15)	-
Lupin + fert.	114 (12)	91 (7)	-
741 stems/ha			
Lupin	56 (14)	32 (8)	-
Fertiliser	73 (13)	116 (12)	-
Lupin + fert.	80 (8)	175 (13)	-

The total ecosystem nitrogen content appears to have determined the patterns of response observed in this experiment. Lupin-derived nitrogen would be incorporated in organic matter which would provide an efficient means of storage and slow release of nitrogen compared to fertiliser. The control plots and, to a lesser extent, the plots with lupin accumulated insufficient nitrogen in the system to provide for the long-term requirements of the trees through bio-geo-chemical cycling. In unthinned stands most of the nitrogen taken up by the trees at age 7 was contained in the foliage, as very little litterfall would have occurred until then. The continued supply of fertiliser nitrogen after canopy closure maintained high rates of leaf production, especially in closed stands, and ensured higher rates of litterfall. Thus, Baker *et al.* (in press) reported litterfall at age 14 ranging between 2.5 and 4.4 t/ha, and 6.7, 11.4, 14.1, and 14.9 t forest floor organic matter/ha in the unthinned control and the stands with lupin, fertiliser, and lupin plus fertiliser, respectively. Litter had an average life of 3 to 4 years, compared with a range of 2 to 12 years for North Island sites in New Zealand, based on litter accumulation and fascicle production data (Carey *et al.* 1982; Madgwick 1985). Forest floor nitrogen content would have increased through thinning, but nitrogen from thinnings does not become available for about 3 or 4 years (Will *et al.* 1983). However, the demand for nitrogen by the tree-crowns would increase immediately after thinning. Because thinning was insufficiently intense to initiate vigorous lupin regrowth and further nitrogen fixation, thinned lupin plots compared poorly to plots receiving fertiliser. Heavy thinning may alter this result. Repeated applications of nitrogen maintained high fascicle production rates which increased the nitrogen content of the forest floor, with long-term consequences for stand growth.

The poor initial response to fertiliser suggests that early additions of nitrogen were utilised inefficiently and largely lost from the system, and that the long-term response to fertiliser must have been largely due to later additions when the trees had more fully occupied the site. Leaching losses were not measured directly but 340 kg N/ha were unaccounted for based on a synthesis of available data from the fertilised stands at age 14 (Baker *et al.* in press). The low organic matter content of Woodhill sandy soils (Gadgil *et al.* 1984) and their low moisture retention characteristics (Jackson, Jackson, & Gifford 1983) both accentuate leaching. As more pine litter (which has a high C/N ratio) accumulates, the nitrogen and moisture retention characteristics of these soils would increase.

The experiment was designed to satisfy nutrient demands of the stand by fertiliser additions. The superior performance of the plots with lupin at age 7 suggests that fertiliser additions did not meet the needs of the trees. Moreover, the large amount of nitrogen unaccounted for at age 14 suggests that matching addition rate to nutrient demand would materially decrease the fertiliser required to obtain maximum growth. In spite of the fact that stands with lupin plus fertiliser nearly matched the growth of highly productive sites in New Zealand, it is not clear whether these stands had optimum nutrition. Thus, foliar-nitrogen concentration dropped over the first 5 years (Gadgil *et al.* 1984) and remained below the normally accepted sufficiency level (Will 1985) even when fertiliser was still being applied. However, fascicle weights were at acceptable levels, even after thinning, implicating factors other than nitrogen supply at Woodhill.

Role of Moisture

Nitrogen supply is concentrated in the forest floor and the top few centimetres of soil, while moisture is available over greater depths. Factors that increase mineralisation might be expected to increase foliar-nitrogen levels. Thus percentage of nitrogen (Gadgil *et al.* 1984) increased with rainfall once stand age effects were removed (H. A. I. Madgwick unpubl. data). Foliar-nitrogen percentage also increased after thinning (R. L. Gadgil pers. comm.), possibly owing to the mulching effect and release of nitrogen from the forest floor, in spite of increased nutrient demands from tree crown expansion and competition with understorey vegetation. The corollary that nitrogen concentration is low in unthinned stands because of poor moisture relations in the litter has not been examined at Woodhill, but decreased forest floor weights have been associated with irrigation (W. J. Dyck pers. comm.). Moisture supply seems to influence foliar-nitrogen concentration at Woodhill through its effect on litter decomposition and nitrogen uptake.

Moisture deficit affects dry matter accumulation at Woodhill. Even in a 42-year-old stand excavation indicated that roots were confined almost exclusively to the upper 5 m of sand (P. N. Beets unpubl. data). Unless the stand had been recently thinned, Jackson, Jackson, & Gifford (1983) found that soil moisture was depleted to critically low levels during late summer and autumn in all but the control stands. Moreover, D. A. Rook (pers. comm.) found that, during a summer drought, tree diameter increment declined in unthinned stands with fertiliser but continued unabated in control stands. Low basal area increments (Jackson, Gifford, & Graham 1983) correspond with dry

summers (Jackson, Jackson, & Gifford 1983). Moisture supply limited pine productivity on this sand-dune site, and on others (Ovington 1950; Wright 1955).

Our data indicate a difference in the nature of the response to increased nitrogen depending on the source, namely fertiliser or lupin. Fertiliser resulted in commensurate increases in crown and stem components. In the presence of lupin, tree crowns responded much more than stems and this differential response resulted in the above-ground dry matter being composed proportionally more of crown matter. We suggest that this difference in response of the pines can be explained by known seasonal shifts in dry matter allocation and seasonal differences in moisture supply. Crown development occurs mainly in spring and early summer (Madgwick 1985) when soil moisture is adequate. Stem growth forms a larger proportion of late summer growth and is more vulnerable to summer depletion of the soil moisture reserves. At Woodhill such depletion occurred when leaf area, of either lupin or pine, was at a maximum. In low-rainfall areas fascicle and stem production and fascicle retention were all influenced by seasonal droughts, especially after fertiliser application without irrigation (Linder *et al.* in press). Indirect effects of fertiliser on moisture supply to the trees may explain the conflicting results in the literature on the effect of nitrogen fertiliser on crown/stem relationships; Cromer, Barr, Williams, & McNaught (1985) reported no effect of fertiliser, while Mead *et al.* (1984) found an increase in crown relative to stem.

CONCLUSIONS

Fascicle production tended to decline with stand age at Woodhill, in agreement with results from productive sites (Madgwick *et al.* 1977; Madgwick & Oliver 1985). Fascicles less than 2 years old tended to increase as a percentage of total fascicle weight after fertiliser application, suggesting a reduction in retention compared with controls. A history of lupin favoured a greater retention of fascicles.

Weights of above-ground tree components increased with increasing nitrogen supply, but were also affected by moisture supply, and so silvicultural treatment involving fertilisers should include considerations of moisture use.

Acceptable levels of growth corresponded with foliar-nitrogen values of about 1.2% between ages 7 and 17 years, suggesting a downward revision of critical foliar-nitrogen levels at Woodhill.

Fertiliser-nitrogen use by the trees is reduced when the potential for leaching is great. The benefits of fertiliser-nitrogen are more likely to be realised on sandy soils after sufficient organic matter has accumulated and the ability of the soil to retain nitrogen has been established.

Organic matter is an important source of nutrients and should be managed accordingly. The quantity of dry matter and nitrogen on the forest floor in the most productive lupin-plus-fertiliser plots is about average for North Island sites and can supply ample nitrogen to maintain growth at Woodhill provided mineralisation is normal.

Thinning increased the proportion of dry matter in crown components. Thinning to waste and stem-only harvesting are useful options for increasing the organic matter content of second-rotation stands.

All thinning treatments were too light to stimulate lupin regrowth. Much heavier thinning would have altered the lupin effect, raising productivity closer to levels associated with similarly thinned stands with fertiliser applied. The initial effects of thinning on the moisture and nitrogen supply to the residual trees through reduced stand evapo-transpiration still apply.

First-rotation stands with lupin only could benefit from the judicious use of nitrogen fertiliser, depending on the tending regime employed. For example, when light or delayed thinning is practised then nitrogen fertiliser application will ensure greater productivity.

Second-rotation stands should be less affected by nitrogen deficiency, assuming that soil and forest floor organic matter is conserved by wise management of the first rotation and careful site-preparation techniques are used. Attention could be focused on increasing water use efficiency at Woodhill.

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