Carbon partitioning in *Pinus radiata* stands in relation to foliage nitrogen status

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Summary First rotation *Pinus radiata* D. Don trees were grown on a nitrogen-deficient sand dune in an experimental design that included lupin (*Lupinus arboreus* Sims) as an understory species, and biennial application of balanced fertilizer in a replicated split-plot factorial design with thinning treatments as subplots. From an initial 2222 stems ha^{-1}, stands were thinned to 1483 and 741 trees ha^{-1} at ages 2 and 4 years, respectively. Mean annual production of foliage, branches, stem, coarse roots, and cones was estimated from measurements of the dry matter content at ages 7, 10, 11 and 17 years. A model was used to estimate total above- and belowground dry matter production from measurements of leaf area index and foliar nitrogen concentration. An estimate of fine root production was obtained from the difference between the model estimate of total production and the estimate of aboveground production.

The fertilizer and lupin treatments increased foliage nitrogen concentration, leaf area index and dry matter production of most aboveground components. In unthinned stands, foliage production ranged from 3 to 6 Mg ha^{-1} $year^{-1}$, branch production from 1 to 4 Mg ha^{-1} $year^{-1}$, and stem production from 8 to 19 Mg ha^{-1} $year^{-1}$, depending on site fertility. Partitioning of aboveground production to foliage, branches, stems, and cones changed with tree age but it was not significantly influenced by the treatments. The fractions of aboveground dry matter production partitioned to foliage, branches, stems and cones were 0.23, 0.12, 0.63 and 0.02, respectively, for trees between ages 7 and 11 years, and 0.21, 0.08, 0.67 and 0.04, respectively, for trees between ages 11 and 17 years. With increasing foliage nitrogen concentration, partitioning to branches increased significantly, whereas partitioning to stems decreased.

The fraction of total dry matter production partitioned to stems decreased significantly with thinning from 0.40 to 0.27 with a concomitant increase in the fraction partitioned to fine roots from 0.31 to 0.46. The average fraction partitioned to fine roots was 0.46 and 0.30 in unfertilized and fertilized stands, respectively. Stem production was more highly correlated with fine root partitioning than with leaf area index. Fine root production was not significantly affected by fertilizer application. The ratio of total net primary production to leaf area index increased significantly with thinning, but not with site fertility or stand age. The ratio of aboveground dry matter production to leaf area index increased with stand age and with the application of fertilizer but not with thinning.

Keywords: forest growth, nitrogen fertilization, plantation forest.

Introduction

Mechanistic growth models are important for investigating the interactions between productivity and nutrient uptake and cycling in forest ecosystems (McMurtrie 1991), and can be used as a predictive tool for assisting decisions on the silvicultural management of production forests. The main limitation to the operational use of such models is that the genetic and environmental controls on carbon and nutrient partitioning to tree components are poorly understood, and data necessary to permit better understanding are difficult to obtain.

In studies where dry matter partitioning to all tree components has been measured, large differences among experimental treatments (e.g., species, tree age, tree spacing, nutritional status, and water availability) have been found (Cannell 1985), but the biological explanation for these differences is uncertain. Substantial sampling error may occur, and estimates of belowground net primary production may be unreliable (Raich and Nadelhoffer 1989). However, there is evidence that reduced carbon partitioning to fine roots increases aboveground production (Linder and Axelsson 1982), and that the response to nitrogen fertilizer results not only from an increase in leaf area index, but also from a change in partitioning of growth from fine roots to aboveground components (Linder and Rook 1984, Cannell 1985).

In *Pinus radiata* D. Don stands growing under conditions of adequate water and nutrient supply at Puruki in central North Island, New Zealand, tree age has a large effect on aboveground partitioning to foliage, branches and stems (Beets and Pollock 1987a). However, the age effect was not changed when intraspecific competition for light was modified by thinning. Furthermore, the ratio of aboveground dry matter production to leaf area index increased with stand age, suggesting that partitioning to fine roots may decrease with increasing tree age (Beets and Pollock 1987a). Data on fine root production

obtained by Santantonio and Santantonio (1987*a*) permit estimates of net primary production to be made for the 12-year-old stands at Puruki, but not for stands of other ages. However, tree age needs to be considered when examining the effects of environmental factors on growth.

We have developed a model to estimate the effects of fertilizer and thinning on above- and belowground carbon partitioning for trees at an experimental site at Woodhill Forest. Detailed aboveground dry matter data were obtained at this site (Beets and Madgwick 1988) during a study of the effects of fertilizer and thinning on productivity and nutrition in mid-rotation-aged stands of *P. radiata*. Estimates of above- and belowground dry matter production were available for a site at Puruki, where it is assumed that water and nutrients are nonlimiting. Measurements of coarse root biomass were available for mature trees at another site in Woodhill Forest. The model was used to estimate total net primary productivity for the experimental site by scaling the data from Puruki in relation to leaf area index and foliage nitrogen concentration. An estimate of fine root dry matter production was calculated as the difference between total net primary production and measured aboveground plus coarse root production.

Methods

Description of sites and experimental treatments

Use was made of measurements from two experimental sites (Sites AK287 and AK 1029) located in stands of *Pinus radiata* growing on a nitrogen-deficient sand dune at Woodhill Forest (36°45′ S, 174°26′E) and a 12-year-old stand growing on a site well supplied with water and nutrients at Puruki (38°26′ S, 176°13′ E), in the North Island, New Zealand. Mean annual temperature was 14 and 11 °C and mean annual rainfall was 1300 and 1500 mm, respectively, at Woodhill Forest and Puruki.

The model provides predictions of dry matter partitioning to fine roots for experimental plots at Site AK287 at Woodhill Forest. This is a first-rotation stand on a dune stabilized by planting *Ammophila arenaria* (L.) Link in June 1965 and sown with *Lupinus arboreus* Sims (tree lupins) in April 1966 to improve site nitrogen fertility. *Pinus radiata* seedlings were planted at 2.4×1.8 m spacing in June 1968 following crushing of the lupin. Treatments included the presence and exclusion of lupin regrowth without added fertilizer and the same treatments with the biennial addition of balanced fertilizer for 10 years. A split-plot factorial design was used (replicated twice), with thinning treatments from 2222 stems ha^{-1} to 1483 stems ha^{-1} at age 2 years or to 741 stems ha^{-1} at age 4 years. The lupin understory had been suppressed by the trees when the current study was initiated. A full description of the experimental treatments and measurements of biomass and nutrient concentrations for the aboveground components at ages 7, 10, 11 and 17 years are given by Beets and Madgwick (1988).

Measurements of coarse root biomass were made in 1986 for a 42-year-old first-rotation stand at Site AK1029, situated close to Site AK287. The stand at Site AK1029 had a history of lupin management similar to that for Site AK287. Following

harvesting, a second-rotation experiment was established in winter 1986. Treatments included different degrees of organic matter removal in a split-plot factorial design with quarterly additions of nitrogen fertilizer as the subplots, as described by Smith et al. (1994). Measurements of photosynthesis were made on 5-year-old trees growing in four plots, consisting of the removal of forest floor organic matter and the addition of extra slash, with or without added fertilizer. These treatments were chosen because the foliage showed a wide range of nitrogen concentrations.

Total net primary production was calculated for a 12-year-old closed-canopy *P. radiata* stand at Puruki from measurements of aboveground production reported by Beets and Pollock (1987*a*, 1987*b*) and measurements of fine root production in the same stand measured by Santantonio and Santantonio (1987*a*).

Calculation of aboveground net primary production

Annual net primary production for the aboveground components, P_a, at Woodhill Forest was calculated from the dry matter content of subplots measured at ages 7, 10, 11 and 17 years by Beets and Madgwick (1988). The numbers of trees used, methods used for subsampling and the scaling procedure to estimate foliage weights by age class, live branch, dead branch, stem and cone dry weights are described by Beets and Madgwick (1988). Mean foliage production was estimated by averaging the weight of foliage up to the age of 1 year at the beginning and end of each measurement period. Mean annual stem, branch, and cone increments were calculated for each sampling period, including losses owing to component mortality. Periodic mean annual net primary production aboveground was calculated by summing foliage, branch, stem and cone production.

Leaf area index

Leaf area index, *l*, for each subplot was determined as decribed by Beets and Lane (1987). Ten fascicles for each foliage age class were selected at random from each sample branch and measured for length and oven dry weight, and an additional random selection of 20 fascicles for each age class were sampled from the entire crown for measurements of volume and dry weight. The mean leaf area index of each subplot was calculated by averaging estimates obtained at the beginning and end of each increment period.

Canopy nitrogen concentration

The mean foliage nitrogen concentration, N, in the three trees per subplot used for biomass measurements at ages 7, 10, 11, and 17 (Beets and Madgwick 1988) was related to foliage nitrogen concentration, N_f, in bulk samples (from 8–10 trees per subplot) of current-year mature foliage from second-order branches collected from the upper crown in February (late summer). The relationship was determined by linear regression analysis to be: $N = 0.58N_f + 3.8$ ($r = 0.84$). This relationship was applied to the subplots using N_f as the driving variable, and was expected to provide accurate predictions of canopy N because N_f was measured annually between stand

ages 2 and 11 years (Gadgil et al. 1984), and at age 15 years (Baker et al. 1986).

Rates of photosynthesis

For 6 days in February 1991, rates of net photosynthesis were measured with a portable photosynthesis system (Model LI-6200, Li-Cor, Inc., Lincoln, NE) on 12 shoots in the upper crown of trees growing in four plots at Woodhill Forest. The nitrogen concentration of the shoots was also determined.

Coarse root production

Coarse root biomass was measured for seven 42-year-old trees at Woodhill Forest Site AK1029, before establishing the second rotation experiment. After felling, roots and stump were extracted by bulldozer. This procedure removed most of the coarse roots (5 to 200 mm diameter) and a variable proportion of the smaller diameter roots (2 to 5 mm diameter). The stump was separated from the coarse roots (defined as roots > 5 mm in diameter, excluding stump). Where roots exceeding 5 mm in diameter were broken, the diameter at the broken tip was measured and the weight of the remainder of the root was estimated from a relationship between diameter and root dry weight of intact roots.

The actual dry weight of these seven coarse root systems fell within 2% of the weight predicted by a relationship between tree diameter at 1.4 m above ground and coarse root biomass developed previously by Jackson and Chittenden (1981) where log(roots > 5 mm diameter) = −5.009 + 2.7296 log(dbh). This relationship was then used to estimate coarse root biomass for each subplot at Woodhill Forest. Periodic mean annual coarse root production was calculated for each sampling period, assuming no mortality.

Model to estimate total net primary production

For a given site, it has been shown that net primary production during a period, P, is linearly related to the integrated solar energy absorbed by the canopy during the same period, G (Linder 1985). For a continuous canopy, it is appropriate to estimate G from measurements of incident solar energy, G_o, using a simple exponential relationship with leaf area index, l (Landsberg 1986). Combining these approaches, it may be expected that:

$$P = \varepsilon G = \varepsilon G_o(1 - e^{-kl}), \qquad (1)$$

where ε is an energy conversion efficiency term. The extinction coefficient, k, is equal to $0.5/\pi$ (Jarvis and Leverenz 1983), where π is a conversion from leaf area on an all-surfaces basis to projected leaf area (Grace 1987). This equation implicitly includes the effects of respiration because it refers to net production and it is assumed that respiration is a constant fraction of photosynthesis (Gallagher and Biscoe 1978).

Measurements of total production, including above- and belowground components, were available for the 12-year-old stand with a closed canopy at Puruki, P_{pur}. The value of P was, therefore, estimated for the subplots at Woodhill Forest by:

$$P = P_{pur}\varepsilon'G_o'(1 - e^{-kl}), \qquad (2)$$

where G_o' and ε' are the ratios of the incident solar radiation and the efficiency of conversion for the two sites. The value of P_{pur} was estimated to be 50 Mg ha^{-1} year^{-1} (Beets and Pollock 1987a), of which 2 Mg ha^{-1} year^{-1} was contributed by fine roots. Mycorrhizal development was known to be minimal (Santantonio and Santantonio 1987a, 1987b). Measurements at Puruki and near Woodhill Forest showed that the long-term annual irradiance at the two sites was very similar. Thus, for the analysis, the value of G_o' was taken to equal one. It was assumed that the value for ε' could be expressed by the ratio of the maximum rates of photosynthesis for the foliage in a subplot to the maximum rate at Puruki.

Fine root production, including mycorrhizal production, was calculated for each subplot for each increment period by subtracting aboveground and coarse root production from the estimated total net primary production.

Statistical analysis

Partitioning of dry matter on aboveground and total net primary production bases for each subplot and increment period was analyzed by a split-plot, randomized block design as described by Beets and Madgwick (1988).

Results

Aboveground production

The presence of lupin and the application of fertilizer increased dry matter production of most aboveground components (Table 1). The fertilizer effects were statistically significant for most components, but only a few of the effects of lupin were significant (Table 1). In unthinned stands, foliage production ranged from 3 to 6 Mg ha^{-1} year^{-1}, branch production from 1 to 4 Mg ha^{-1} year^{-1}, and stem production from 10 to 19 Mg ha^{-1} year^{-1}, depending on site fertility (Table 1).

Partitioning of dry matter to foliage, branches, stem, and cones was not significantly different among nutritional treatments ($P = 0.05$). Average fractions of dry matter partitioned to foliage, branches, stems and cones were 0.23, 0.12, 0.63 and 0.02, respectively, between ages 7 and 11 years, and 0.21, 0.08, 0.67 and 0.04, respectively, between ages 11 and 17 years (Table 2). However, thinning resulted in a reduction in partitioning to stem and an increase in partitioning to branches, especially where fertility was higher ($P = 0.1$). The differences in partitioning between treatments become more apparent when the data were plotted in relation to foliage nitrogen concentration, N_f (Table 3). As N_f increased, partitioning to branches increased at the expense of stems, whereas partitioning to foliage was unaffected (Figure 1). Data obtained over 2 years from the 12-year-old stand at Puruki (Beets and Pollock 1987b), where N_f was high, are also included in Figure 1.

The effects of treatments on the ratio of aboveground production to leaf area index, γ, are shown in Table 3. For the mean of the fertility treatments, thinning from 2222 to 741 stems

Table 1. Periodic mean annual dry matter production for tree components at Woodhill Forest for stand ages between 7 and 11 years at tree spacings of 2222, 1483, and 741 stems ha^{-1}, and for stand ages between 11 and 17 years at a tree spacing of 2222 stems ha^{-1}. Total production was estimated from the model, and fine root production is the difference between total and estimated aboveground components. Abbreviations for the plots are: C = control, L = presence of lupin, F = fertilizer added, LF = lupin and fertilizer, and S = thinning treatment. The negative sign refers to a significant negative response. The probability of significant differences between the treatments and their interactions is shown by asterisks, where * denotes $P = 0.05$ and ** denotes $P = 0.01$.

Treatment	Stems ha^{-1}	Dry matter production (Mg ha^{-1} year^{-1})						
		Foliage	Branch	Stem	Cones	Coarse root	Fine root (est.)	Total
Stand age: 7 to 11 years								
C	2222	3.0	1.9	9.7	0.3	1.4	10.4	26.8
L	2222	4.5	1.2	12.3	0.2	2.1	13.4	33.7
F	2222	5.3	2.7	13.4	0.5	2.9	10.2	35.0
LF	2222	5.9	3.5	18.5	0.5	3.8	5.9	38.1
C	1483	2.9	1.9	8.2	0.3	1.6	11.1	25.9
L	1483	3.9	1.6	10.0	0.2	2.3	15.0	33.0
F	1483	4.9	2.6	16.3	0.5	3.0	8.5	35.8
LF	1483	4.7	1.3	12.6	0.2	3.0	13.3	35.1
C	741	2.4	0.8	5.8	0.2	1.5	15.2	25.9
L	741	4.0	1.6	7.9	0.3	2.2	17.7	33.7
F	741	4.0	2.9	11.5	0.5	3.0	12.8	34.8
LF	741	5.4	4.3	11.1	0.3	3.2	14.1	38.5
		F*		F**	F**	F**	S*	F**
		S**		−L**	L**	S**		L**
		L×S*		L×S*	F×L*			F×L*
Stand age: 11 to 17 years								
C	2222	2.8	0.6	8.1	0.5	1.1	13.0	26.1
L	2222	3.6	1.9	13.6	1.0	1.7	10.5	32.2
F	2222	5.2	2.4	16.4	0.8	1.6	7.2	33.6
LF	2222	6.1	2.8	18.1	0.6	2.7	6.9	37.2
		F*	F*	F*		F**		F*
						L**		L*

ha^{-1} resulted in reductions in *l* and stem production of 20 and 33%, respectively, although the production of current-year foliage in the thinned plots was the same as in the unthinned plot (Table 1). The ratio, γ, increased with addition of fertilizer and with stand age. However, it decreased in thinned stands where lupin was present. This was probably a result of the decrease in N$_f$ following suppression of the lupin understory by trees in the unfertilized stands (Gadgil et al. 1984), and the low rates of new foliage production in these subplots (Beets and Madgwick 1988). The ratio did not increase with thinning, even though *l* was lower in thinned plots than in unthinned plots.

Rates of photosynthesis

Maximum rates of photosynthesis, A_{max}, defined as the rate occurring when incident quantum flux density during the measurement was greater than 1000 µmol m^{-2} s^{-1}, ranged from 1 to 4 µmol m^{-2} s^{-1} and were generally low, which is consistent with the low foliage nitrogen concentrations (Table 3). Combining the data for all treatments and canopy positions resulted in a linear relationship between increasing A_{max} and increasing foliage nitrogen concentration (Figure 2). Average canopy nitrogen concentration in each subplot, estimated

by regression from N$_f$ (Table 3) and the data in Figure 2, gave values of A_{max} at Woodhill Forest between 0.65 and 0.84 times the values at Puruki (Grace et al. 1987), where average canopy nitrogen concentration is 15 mg g^{-1} (Beets and Pollock 1987*b*). The values of ε' in Equation 2 were estimated from the ratios of A_{max} for each subplot at Woodhill to the value of A_{max} at Puruki.

Root production and partitioning of net primary production

The rates of production of coarse roots, calculated according to the relationship given by Jackson and Chittenden (1981), are shown in Table 1. The significant treatment effects simply reflect the effect of nutritional treatments on stem diameter.

There were no statistically significant effects of nutritional treatments on estimates of fine root production (Figure 3), although fine root production was greater in thinned stands than in unthinned stands (Table 1). However, the fraction of production partitioned to fine roots, η$_r$, was lower for fertilized plots (0.30) than for the control plot and plots with lupin only (0.46). The value of η$_r$ increased with thinning from 0.31 for the plots at 2222 stems ha^{-1} to 0.46 for plots at 741 stems ha^{-1} (Table 3). There was a significant decrease in η$_r$ with increasing N$_f$ (Figure 3), but the relationship changed with stand age

Table 2. Fraction of aboveground periodic mean annual production partitioned to foliage, branch, stem and cones at Woodhill Forest for stands between 7 and 11 years at tree spacings of 2222, 1483, and 741 stems ha^{-1}, and between 11 and 17 years at a tree spacing of 2222 trees ha^{-1}. Abbreviations for the plots are: C = control, L = presence of lupin, F = fertilizer added, LF = lupin and fertilizer, and S = thinning treatment. The negative sign refers to a significant negative response. The probability of significant differences between the treatments and their interactions is shown by asterisks, where * denotes $P = 0.05$ and ** denotes $P = 0.01$.

Treatment	Stems ha^{-1}	Fraction of annual production partitioned:			
		Foliage	Branch	Stem	Cones
Stand age: 7 to 11 years					
C	2222	0.20	0.12	0.65	0.02
L	2222	0.25	0.07	0.67	0.01
F	2222	0.25	0.12	0.61	0.02
LF	2222	0.21	0.12	0.66	0.02
C	1483	0.21	0.15	0.62	0.02
L	1483	0.25	0.11	0.63	0.01
F	1483	0.20	0.11	0.67	0.02
L	1483	0.25	0.07	0.67	0.01
C	741	0.26	0.08	0.64	0.02
L	741	0.29	0.12	0.57	0.02
F	741	0.21	0.15	0.60	0.03
LF	741	0.25	0.20	0.53	0.02
				−S*	−L*
Stand age: 11 to 17 years					
C	2222	0.24	0.05	0.68	0.04
L	2222	0.18	0.09	0.68	0.05
F	2222	0.21	0.10	0.66	0.03
LF	2222	0.22	0.10	0.66	0.02

Table 3. Foliage nitrogen concentration, N_f, for current-year mature foliage from second-order branches in the upper crowns of eight to 10 trees measured in February, leaf area index, l, ratio of aboveground production to leaf area index, γ, and the fraction of production partitioned to fine roots, η_r, at Woodhill Forest for stands between 7 and 11 years at tree spacings of 2222, 1483, and 741 stems ha^{-1}, and between 11 and 17 years at a tree spacing of 2222 trees ha^{-1}. Abbreviations for the plots are: C = control, L = presence of lupin, F = fertilizer added, LF = lupin and fertilizer, and S = thinning treatment. The negative sign refers to a significant negative response. The probability of significant differences between the treatments and their interactions is shown by asterisks, where * denotes $P = 0.05$ and ** denotes $P = 0.01$.

Treatment	Stems ha^{-1}	N_f (mg g^{-1})	l	γ	η_r
Stand age: 7 to 11 years					
C	2222	8.1	10.6	1.40	0.39
L	2222	10.8	15.5	1.18	0.40
F	2222	11.0	17.4	1.25	0.29
LF	2222	12.6	19.6	1.44	0.15
C	1483	8.8	9.2	1.42	0.44
L	1483	10.7	14.3	1.10	0.45
F	1483	12.2	15.5	1.57	0.24
LF	1483	11.5	15.7	1.20	0.38
C	741	9.3	8.6	1.06	0.59
L	741	12.0	13.5	1.07	0.53
F	741	12.8	13.2	1.51	0.36
LF	741	13.6	16.8	1.25	0.37
		F**	F*	F*	−F*
		L*	−S*	−L*	S**
		S**			
		F×L*			
		L×S*			
Stand age: 11 to 17 years					
C	2222	8.3	9.8	1.22	0.50
L	2222	10.1	14.4	1.40	0.33
F	2222	10.4	16.4	1.50	0.22
LF	2222	12.1	19.4	1.43	0.19
		F*	F*		
		L*	L*		

and intensity of thinning. Stem production decreased with increasing η_r (Figure 4), and the correlation coefficient for this relationship was greater than for the relationship between stem production and l (Figure 4).

Discussion

The data on partitioning of aboveground dry matter production for stands with different fertilities complement the relationships reported for fertile sites at Puruki (Beets and Pollock 1987a). Overall, the patterns were similar and dominated by effects related to tree age. For example, partitioning to foliage was apparently unaffected by fertility or thinning, which is consistent with the results from Puruki at the same age. However, at low values of N_f, partitioning of aboveground production to branches decreased relative to that to stems (Figure 1). Values of N_f increased with thinning, and the improved nitrogen status may have resulted in increased partitioning to branches (Table 2). Increased branch production relative to stem production has been observed previously for *Pinus radiata* under conditions of high nitrogen (Will and Hodgkiss 1977, Mead et al. 1984, Smith et al. 1994) and also in *Pseudotsuga menziesii* (Mirb.) Franco (Brix 1981).

The data from Puruki provide the only estimate of net primary productivity including coarse and fine roots for *P. radiata*. The use of these data in the estimate of total productivity for Woodhill Forest involved several assumptions. The estimate of 50 Mg ha^{-1} year^{-1} as the potential production is somewhat arbitrary. However, at a site where irrigation and nitrogen fertilizer were applied to *P. radiata*, the maximum aboveground net primary production was 39 Mg ha^{-1} year^{-1} (Snowdon and Benson 1992), which is much larger than the reported values, for irrigated and fertilized stands, of 15 Mg ha^{-1} year^{-1} for *Pinus elliottii* Engelm. (Gholz et al. 1991) and 12 Mg ha^{-1} year^{-1} for *Pseudotsuga menziesii* (Gower et al. 1992). A value greater than 50 Mg ha^{-1} year^{-1} would correspondingly increase fine root production. The predicted amount of fine root production for *P. radiata* at Woodhill exceeds estimates of belowground net primary productivity for
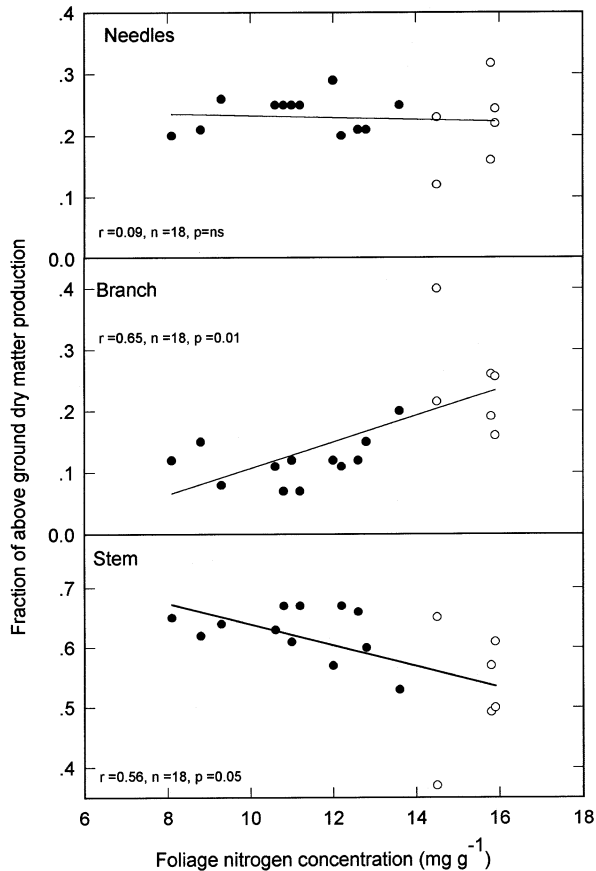
Figure 1. Fractions of aboveground dry matter production partitioned to foliage, branches, and stem in relation to foliage nitrogen concentration. The data are shown for trees between 7 and 11 years old at Woodhill Forest (solid symbols). Also shown are data for a site with high foliage nitrogen concentrations at Puruki (open symbols).
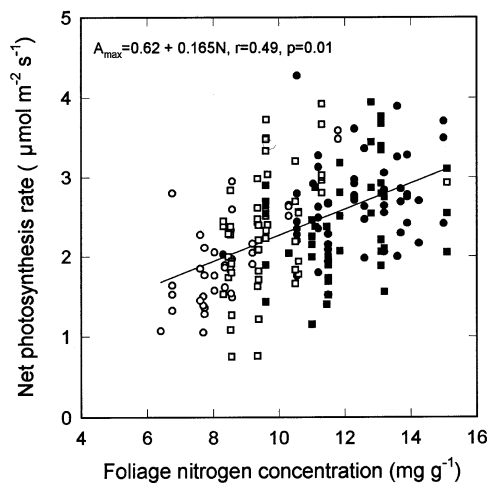

Figure 2. Rates of maximum photosynthesis, A_{max} (μmol m^{-2} s^{-1}), in relation to foliage nitrogen concentration, N (mg g^{-1}), for samples distributed through canopies for subplots in four treatments. The symbols refer to different treatments where ○ removal of lupins, ● removal of lupins with added fertilizer, □ addition of extra slash and ■ addition of extra slash and fertilizer.
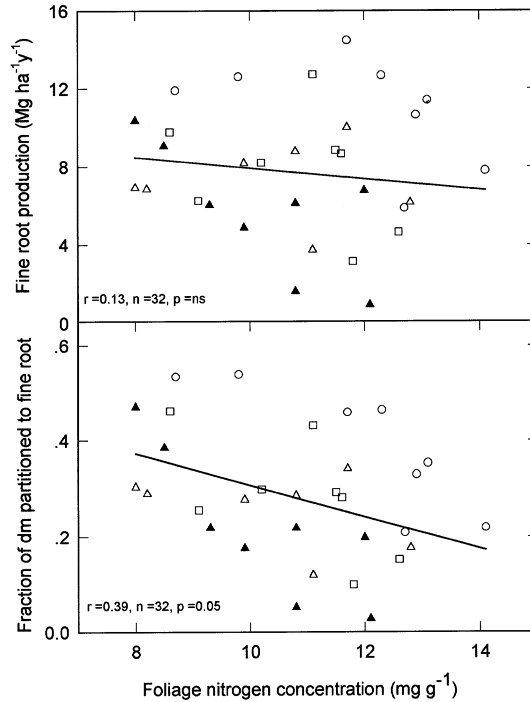
Figure 3. Estimated fine root production and the fractional partitioning of total dry matter (dm) to fine roots in the sub-plots in relation to foliage nitrogen concentrations. The open symbols are for trees between 7 and 11 years old from different thinning treatments where △ is 2222 stems ha^{-1}, □ is 1483 stems ha^{-1} and ○ is 741 stems ha^{-1}. The closed symbol ▲ refers to trees between 11 and 17 years old at 2222 stems ha^{-1}. The data with the same symbol were taken from subplots with different nutritional treatments.

other pine forests, which range from 0.1 to 9 Mg ha^{-1} year^{-1} (Gower et al. 1994); however, aboveground productivity of *P. radiata* also exceeds rates reported for other pine species. At Woodhill, the fraction of production partitioned to roots is consistent with partitioning estimates for other species, after allowing for nutritional differences (Cannell 1985), which gives confidence to the large estimates for fine root production. At Puruki, the standing crop of live fine roots was only 1.4 Mg ha^{-1}, mychorrizal development was minimal (Santantonio and Santantonio 1987b), and fine root production was estimated to be 2 Mg ha^{-1} year^{-1} (Santantonio and Santantonio 1987a). Thus, in view of the high nitrogen status of the trees, total production is unlikely to have been greater than that estimated.

Two further assumptions in estimating productivity at Woodhill were the scaling of total productivity from Puruki based on leaf area index and the use of the ratio of maximum rates of photosynthesis to define ε' in Equation 2. The simple exponential model for scaling by leaf area index in Equation 2 is justified for closed canopies on the basis of the relationship observed between net primary production and absorbed solar energy at other sites (Landsberg 1986). In several studies with conifers, the energy conversion efficiency has been shown to increase with the addition of fertilizer and irrigation (Raison and Myers 1992).
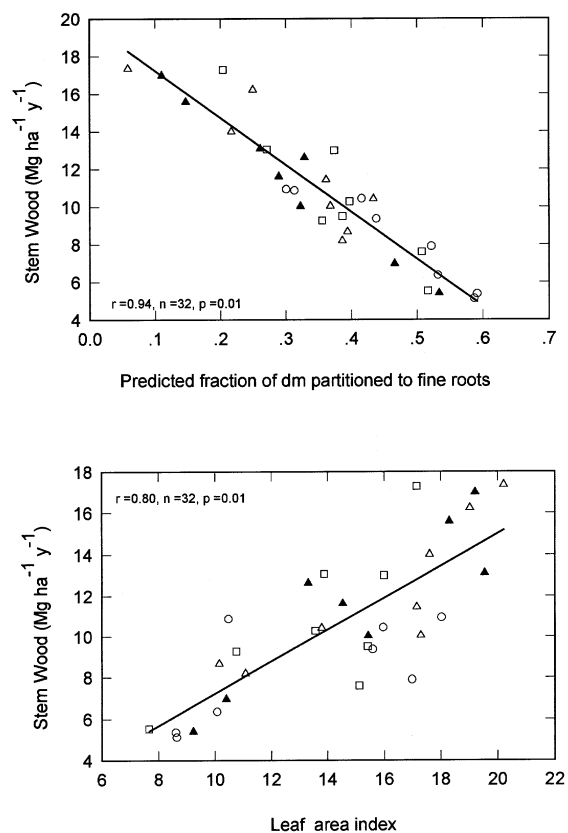
Figure 4. Stem wood production in relation to the fraction of dry matter (dm) partitioned to fine roots and leaf area index for the subplots. The symbols and terminology are the same as those in Figure 3.

Maximum rates of photosynthesis, A_{max}, were consistent with those reported for unfertilized and fertilized but non-irrigated stands in eastern Australia (Thompson and Wheeler 1992). The slightly higher A_{max} measured at Puruki (cf. Grace et al. 1987) is consistent with the relationship between A_{max} and foliage nitrogen concentration (Figure 2). The increase in A_{max} associated with high foliage nitrogen concentrations was less than the increase in l in response to fertilizer. Thus, for a 7–11-year-old unthinned stand, the increase in l between the control plot and the plot with lupin and fertilizer added was 85%, whereas the equivalent increase in A_{max} predicted from Figure 2 was 33%. This is consistent with the observation that nitrogen fertilization increases productivity predominantly by increasing foliage area (Vose and Allen 1988, Gholz et al. 1991). Thompson and Wheeler (1992) showed that A_{max} in *P. radiata* increased with increasing foliage nitrogen concentration when stomatal conductance was high. However, Sheriff et al. (1986) showed that there was no effect of foliage nitrogen concentration on A_{max} in *P. radiata*, and Teskey et al. (1994) showed that it had very little effect in *Pinus elliottii*. It is possible that values of A_{max} at Woodhill may have been overestimated for treatments with high values of l because the development of summer water deficits can occur in some years (Jackson et al. 1983); however, this effect would result in a

further increase in partitioning to roots in the nitrogen-deficient subplots.

The strong negative relationship between stem growth and partitioning to fine roots (Figure 4) supports the view of Linder and Rook (1984) that the response to fertilizer results from a change in partitioning as well as an increase in l. An increase in site fertility following fertilization appeared to stimulate aboveground production without markedly affecting fine root production, and consequently the fraction of net primary production allocated to fine roots decreased with increasing foliage nitrogen status (Figure 3). The range in η_r evident in Figure 3 is related to the nutritional treatments (cf. Gower et al. 1994). Thinning appeared to increase partitioning to fine roots (Table 3), and this may explain why growth responses to nitrogen fertilizer are more likely to occur following thinning (Hunter et al. 1985). A small increase in partitioning to root production following thinning was found at Puruki even though the nitrogen status was high (Santantonio and Santantonio 1987a). The results show complicated interactions among nutritional treatments and tree spacing, and confirm the importance of relating partitioning patterns directly to foliage nitrogen concentration.

The approach used suggests that a reduction in partitioning of net primary production to fine roots is a major determinant of the aboveground response to nitrogen fertilizer. It also appears that thinned stands require higher foliage nitrogen concentrations than unthinned stands to achieve maximum growth rates.

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