RESPONSE TO FERTILISER IN A PINUS RADIATA PLANTATION. 2: ACCUMULATION AND PARTITIONING OF NUTRIENTS

R. N. CROMER, N. J. BARR, and D. TOMPKINS
Division of Forest Research, CSIRO, P.O. Box 4008,
Queen Victoria Tce, A.C.T. 2600, Australia

(Received for publication 23 August 1984; revision 14 February 1985)

ABSTRACT

An application of 67 kg phosphorus/ha to a plantation of **Pinus radiata** D. Don shortly after planting, increased the above-ground biomass from 63 t/ha to 117 t/ha. Differences between unfertilised and fertilised trees in nutrient uptake were of a similar magnitude for nitrogen, phosphorus, and potassium.

The way in which the nutrients were distributed amongst the biomass components differed substantially for nitrogen, phosphorus, and potassium but differences between treatments were small. Needles contained the highest proportion of the three nutrients examined; in fertilised trees they contained some 50% of the nitrogen and 40% of the phosphorus but only about 30% of the potassium. The stem wood and stem bark together contained some 50% of the potassium.

There was a decrease in the concentrations of nitrogen, phosphorus, and potassium from the top to the base of the green crown within one age-class of needles. Although it was less marked, there was also a decrease in nutrient concentration with increasing age of needles. Trees which were severely deficient in phosphorus showed little variation in the concentration of this element in the crown, whereas trees with higher nutrient status exhibited steeper gradients in nutrient concentrations.

Phosphorus concentrations in the current foliage of trees which received 67 kg P/ha showed a substantial decline between the ages of 4 and 6 years. This internal dilution occurred earlier where less fertiliser had been applied, but did not occur where a heavier application had been made. The phosphorus concentrations in current foliage, litter, and soil (exchangeable), all provided reliable estimates of the current phosphate status of **P. radiata** aged 10 years.

Keywords: biomass; nutrient accumulation; nutrient partitioning; nitrogen; phosphorus; potassium.

INTRODUCTION

Pinus radiata has been grown extensively in Australia and New Zealand as a plantation crop to supplement the dearth of native softwoods in both countries. Growth rates of the exotic conifer have generally been more rapid than the native vegetation which it replaced and fears have sometimes been expressed that the plantations would lead to depletion of nutrients from the sites (e.g., Feller 1978).

The nutrient content of various components in *P. radiata* has been examined by a number of workers over the last 30 years (e.g., Will 1957, 1964; Oman & Will 1960; Raupach 1967; Stewart *et al.* 1981). In the most comprehensive study, the concentrations of eight nutrients in the above-ground components of *P. radiata* were examined in an age series from 2 to 22 years (Madgwick *et al.* 1977). Nutrient contents increased rapidly up to the time of canopy closure at about 6 years of age, but increased only gradually thereafter (excluding the effect of a thinning to waste, which caused a sudden drop).

Three distinct nutritional stages in the life of a forest have been recognised by Miller (1981). During the years prior to canopy closure (Stage 1) tree growth is predominantly dependent on soil nutrients, and responses to a number of nutrients can be expected. After canopy closure (Stage 2), responses are unlikely unless leaf area has decreased after thinning or drought and tree canopies have to be reconstructed. Immobilisation of nutrients in the biomass and litter as trees age (Stage 3) can lead to the development of deficiencies, such as that which occurs with nitrogen in coniferous forests of the Northern Hemisphere.

Most fertiliser responses which have been reported in *P. radiata* have been initiated during the period prior to canopy closure (Stage 1 of Miller 1981), when responses would most be expected (e.g., Waring 1973). There have been some instances in which responses have occurred after thinning (Stage 2) when the crown biomass was being re-established (e.g., Crane 1981).

Plantations of *P. radiata* have frequently been established on infertile soils and at least part of the reason for the second-rotation decline in South Australia (Keeves 1966) has now been recognised as depletion of nutrients during harvesting and site preparation for re-establishment (Woods 1980). Despite this recognition, and the knowledge that substantial growth responses can be obtained from the application of fertiliser on many sites, few accounts have been published which compare the uptake and partitioning of nutrients in fertilised and unfertilised stands.

In one study, however, Flinn *et al.* (1982) examined the biomass and the phosphorus concentrations in a 7-year-old stand of *P. radiata* which had received three levels of superphosphate at 4 years of age. The application of fertiliser was associated with increases in above-ground biomass and also in the phosphorus content of each component. The proportion of phosphorus in most components of the trees showed little variation between treatments, but it increased in the needles and branches of the upper crown with increasing rates of fertiliser application (Flinn *et al.* 1982).

This paper describes the effect of fertiliser application on the accumulation and partitioning of nitrogen, phosphorus, and potassium in a 10-year-old plantation of *P. radiata* which received a range of fertiliser treatments in the first few years after planting. The effect of these treatments on early growth and the predicted economic returns have been reported previously by Cromer *et al.* (1977) and Dargavel & Cromer (1979).

MATERIALS AND METHODS

Field

The experiment was planted in winter 1971 at a site 13 km south-east of Traralgon, Victoria, Australia (38° 16'S, 146° 40'E). A detailed description of the experimental site, fertiliser treatments, and methods has been given by Cromer *et al.* (1985). Weeds

were controlled in four of the five blocks and data are presented only for these. The site had previously carried a stand of *P. radiata* and was known to be deficient in both phosphorus and potassium, and so detailed examination of nutrients concentrated on the macro-elements – nitrogen (N), phosphorus (P), and potassium (K).

Each block contained 12 plots; three were unfertilised controls (P_0), and the other nine were treated with one of three fertiliser types (phosphorus alone, nitrogen + phosphorus, or nitrogen + phosphorus + potassium with trace elements) at one of three application levels. The soil was a typical soloth (Stace *et al.* 1972) and has been classified as Maryvale sandy loam (Turvey & Poutsma 1980), with an A horizon of shallow loamy sand (30–50 cm) and an abrupt boundary to the clay B horizon.

Biomass and stand data from the four fertiliser treatment levels have already been reported (Cromer *et al.* 1985) but as sample trees were removed only from P_0 (five trees) and P_2 (15 trees) treatment levels, nutrient uptake and partitioning data in this paper are reporetd only for these treatments. The P_2 treatment included trees from the three fertiliser types (P_2, N_2P_2, and $N_2P_2K_2$). Standing (forest floor) litter and soil samples were collected from all 48 plots so these data refer to all treatments. Samples of current foliage which had been removed from all plots on four occasions during the 10 years prior to the biomass sampling also refer to all treatment levels.

Methods used which are relevant to the nutrient aspects of the experiment are described below.

Samples of current needles from the upper crown were removed for chemical analysis in May 1973, July 1975, May 1978, and April 1981 when the trees were aged 2, 4, 7, and 10 years. Nutrient concentrations in needles vary with season but are relatively stable during the autumn-winter period (Raupach 1967; Fife & Nambiar 1982). On each of these occasions, foliage samples were removed from six co-dominant trees in each plot at a standard position (upper crown, lowest whorl with one age of needles).

Standing litter samples were removed from an area of 0.1 m^2 using a cylindrical metal cutter and, as weed control had been effective, living vegetation was virtually absent. Two composite samples, composed of six randomly located sub-samples, were removed from each plot, taken to the laboratory, and dried as for the biomass samples. The composite samples were stratified as (a) within the mounds and (b) between the mounds, to provide an estimate of within-plot variation. Soil samples were taken at the locations where standing litter had been removed. Hollow tubes 25 mm in diameter were used to remove samples from the 0–10, 10–20, and 20–40 cm depths (Veihmeyer 1929). Two composite samples, each composed of six sub-samples, were removed from each depth in each plot. Samples for each depth were removed from the same hole so depth was confounded within sample location.

Laboratory

The green crown had been divided into five sections of equal length and two sample branches removed from each section. Needles were removed from each sample branch and separated into four age-classes (0–1 year, 1–2 years, 2–3 years, and >3 years). Sub-samples of all components including stem wood, stem bark, dead branches, live branches, dead needles, live needles, and female cones were dried at 75°C to constant

weight. The total mass (oven-dry) for each component was determined from the ratio of fresh to dry mass measured on the sub-samples.

Representative sub-samples of each component were ground for chemical analysis. Needle samples of each age-class from each branch were kept separate, but a composite sample of the wood and bark from each branch sample was ground for analysis. Wood discs and bark from 0.2, 0.5, and 0.8 of total height were subjected to chemical analysis. In order to reduce the number of chemical analyses required, the wood samples were divided into two groups. Segments of wood from pith to bark of 12 trees (three per treatment) were used to determine average nutrient values for each third of the tree stem. Wood discs from the remaining eight trees (two per treatment) were cut into rings containing 2 years of growth to determine nutrient values for different ages of wood.

Samples of plant material were digested in glass tubes over a heated aluminium block with sulphuric acid and hydrogen peroxide (Lowther 1980). Nitrogen was distilled from the diluted digest as ammonia, absorbed in boric acid, and the quantity determined by titration. Phosphorus in the digest was determined colorimetrically using the molybdate blue method. Potassium was determined using a flame photometer.

Soil samples were air-dried and sieved to remove gravel over 2 mm in diameter. Soil pH was measured after shaking the samples for half an hour with de-ionised water (soil mass : solution volume ratio of 1 : 2). Electrical conductivity was also measured on this solution after further dilution to a soil : solution ratio of 1 : 5. Phosphorus was extracted in acidified ammonium fluoride and determined colorimetrically as the molybdenum complex (called Bray No. 2, Bray & Kurtz 1945). Cation exchange capacity was determined by leaching the soil with ammonium acetate at pH 7. Exchangeable cations were determined after removing soluble cations with alcohol. A small sub-sample of soil was ground in a mortar to pass a 246-μm sieve and used for the determination of organic matter by wet oxidation (Walkley & Black 1934). Soil nitrogen was converted to ammonium by micro-kjeldahl digestion and determined colorimetrically.

Statistical Analyses

Sample trees had been removed from the unfertilised control (P_0) and the three fertiliser types (P_2, N_2P_2, and $N_2P_2K_2$) and these data were subject to analysis of variance on this basis. Differences between the three treatments which received fertiliser were rarely significant, and so results for the P_0 plots have generally been compared with the three fertiliser "types" combined (P_2).

Needle biomass and nutrient concentration data (on an individual tree basis) were subjected to a split-plot analysis of variance, with needle age-class nested within sections of the green crown, which were in turn nested within treatments as shown in Table 1. Data were analysed using the statistical program GENSTAT (Genstat Manual 1977). Some age-classes of needles were not always present (e.g., old needles in the upper crown) and, in order to obtain an estimate of the mean nutrient concentration for each unit, these were interpreted as missing values. In the analysis of variance for needle biomass, missing values were interpreted as zeros.

The analysis of variance of individual sample trees showed that fertiliser treatment significantly ($p < 0.01$) increased the concentration of phosphorus in the needles, but did not significantly influence the concentrations of nitrogen or potassium, or the biomass of live needles (Table 1). The sample trees were chosen at random from five diameter classes in order to calculate regression equations and not to represent treatment means. The concentrations of the three nutrients and the biomass of the needles were influenced by the section of the crown in which they occurred and their age ($p < 0.001$) and there was a significant interaction between age-class and section ($p < 0.01$, Table 1).

TABLE 1—Analysis of variance for needle biomass and the concentrations of nitrogen, phosphorus, and potassium in the live needles of **P. radiata** aged 10 years. The needles from each of 20 trees were separated into four age-classes within five sections of the green crown

Variable	d.f.	Biomass	N	P	K
Fertiliser	3	NS	NS	**	NS
Residual	16				
Section	4	***	***	***	***
Sect . Fert	12	NS	NS	NS	NS
Residual	64				
Age	3	***	***	***	***
Age . Fert	9	***	NS	NS	NS
Sect . Age	12	***	**	***	**
Age . Fert . Sect	36	NS	*	NS	NS
Residual	240				

NS not significant
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

Data for live branches, stem bark, and stem wood were also subjected to a split plot analysis of variance with section nested within treatments (Table 2). Live branches were divided into five crown sections as for needles. On a sample tree basis, fertiliser treatment did not have a significant effect on branch biomass or nutrient concentration but both these parameters were significantly influenced by position in the crown ($p < 0.001$).

RESULTS

The concentrations of nitrogen, phosphorus, and potassium in the needles of the five sections of the crown are shown in Fig. 1a,b,c. Age-classes 0–1 and 2–3 years only are shown for clarity and treatments are combined for nitrogen and potassium as differences were not significant. Within a particular age-class, the concentrations of both nitrogen and potassium decreased with decreasing vertical position in the green

TABLE 2—Analysis of variance table of biomass and nutrient concentrations in the live branches, stem bark, and stem wood of **P. radiata** aged 10 years. Branches from 20 trees were divided into five crown sections as for needles. Bark and wood biomass data represent 10 stem sections whereas nutrient data were derived from only three points up the stem

Variable	Live branches					Stem bark						Stem wood					
	d.f.	BM	N	P	K	d.f.	BM	d.f.	N	P	K	d.f.	BM	d.f.	N	P	K
Fertiliser	3	NS	NS	NS	NS	3	NS	3	NS	NS	NS	3	*	3	NS	NS	NS
Residual	16					16		16				16		8			
Section	4	***	***	***	***	9	***	2	***	***	***	9	***	2	***	***	***
Sect . Fert	12	NS	NS	NS	***	27	**	6	NS	NS	NS	27	***	6	NS	NS	NS
Residual	64					144		32				144		16			

BM biomass
NS not significant
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

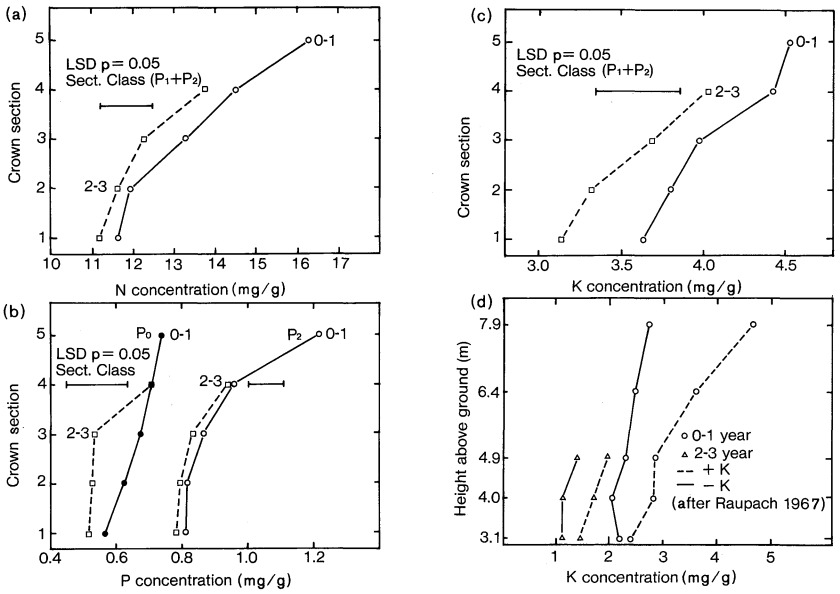

FIG. 1—The concentrations of nitrogen (a), phosphorus (b), and potassium (c) in the live needles of **P. radiata** aged 10 years, by section of the crown. Age-class 0–1 year (°———°), 2–3 years (□- - - -□). Fertilised and unfertilised plots are shown separately for phosphorus but not for nitrogen and potassium as the treatment effect was not significant. Potassium concentrations from data presented by Raupach (1967) are shown in (d).

crown. The concentrations of nitrogen and potassium also fell as needle age increased, but differences within a particular section of the crown were less marked than differences between sections of the crown. Data for phosphorus concentrations are shown separately for each treatment as this effect was significant. The gradient in phosphorus concentration from the top of the crown to the base was steeper in fertilised trees than in unfertilised.

The fraction of the total live needle biomass, calculated on an individual tree basis, for each age-class of needles within each section of the crown and each treatment (derived from the Anova in Table 1) was multiplied by the total live needle biomass for each treatment on an area basis (Table 3, and Cromer *et al.* 1985) and the results are shown in Fig. 2a. The influence of the larger trees and better survival in the fertilised plots is apparent when data are presented on an area basis. The fertilised plots contained a greater mass of needles in virtually every section of the crown and age-class of needles than the unfertilised plots. Trees in fertilised plots also contained a higher percentage of needles more than 3 years old, indicating they held their needles longer than unfertilised trees.

To obtain an estimate of the mass of each nutrient in the needles, the nutrient concentration of each sample was multiplied by the mass of that sub-component (age-class, section, and treatment) with missing observations treated as zeros. Nutrient mass

TABLE 3—Above-ground biomass and accumulation of major nutrients in the components of **P. radiata** aged 10 years

Variable	Biomass (t/ha)		Nutrients (kg/ha)					
			Nitrogen		Phosphorus		Potassium	
	P_0	P_2	P_0	P_2	P_0	P_2	P_0	P_2
Stem wood	39.7	71.4	23.4	38.3	1.43	2.72	21.3	37.6
Stem bark	6.3	12.3	25.2	45.4	2.20	4.23	19.7	32.8
Branches:								
Live	6.6	13.1	18.9	42.4	1.42	3.96	11.4	24.2
Dead	0.4	5.9	1.0	9.0	0.04	0.62	0.2	2.6
Needles:								
Live								
Branch	7.9	9.7	95.3	127.6	4.90	8.82	27.6	39.3
Stem	0.1	0.2	1.8	2.4	0.09	0.22	0.5	0.6
Dead	0.2	1.7	1.3	11.4	0.05	0.67	0.9	1.1
Cones	2.0	3.0	6.5	8.3	0.90	1.86	2.1	3.1
Total	63.2	117.3	173.4	284.8	11.03	23.10	83.7	141.3
Total live*	60.6	106.7	164.6	256.1	10.04	19.95	80.5	134.5

* Total live excludes dead needles, dead branches, and cones.

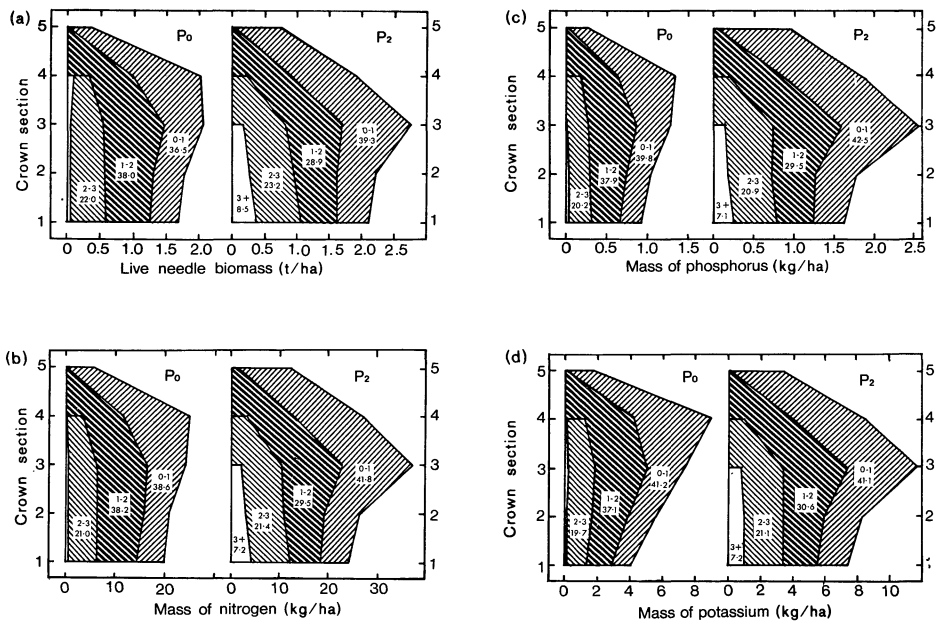

FIG. 2—Needle biomass (a) and the mass of nitrogen (b), phosphorus (c), and potassium (d) in the needles of unfertilised and fertilised plots of **P. radiata** aged 10 years. Data are divided into four age-classes within five crown sections of equal length. Figures in brackets are the percentages of the total represented by each age-class.

for each sub-component was converted to an area basis in the same way as needle biomass. The mass of nitrogen, phosphorus, and potassium in each crown section and age-class are shown in Fig. 2b,c,d respectively.

Live branch biomass was converted to an area basis in the same way as the needle data, and fertilised plots contained substantially more than unfertilised plots (Fig. 3a). The concentrations of nitrogen in the branches of each crown section were substantially lower than the concentrations in the needles but decreased from the top of the crown to the base in the same way as the needles (Fig. 3b). The concentrations of phosphorus and potassium in the live branches were closer to the values of these elements in the needles, with the branches in the upper crown having concentrations which were equal to or exceeded those in the lower needles (Fig. 3c,d).

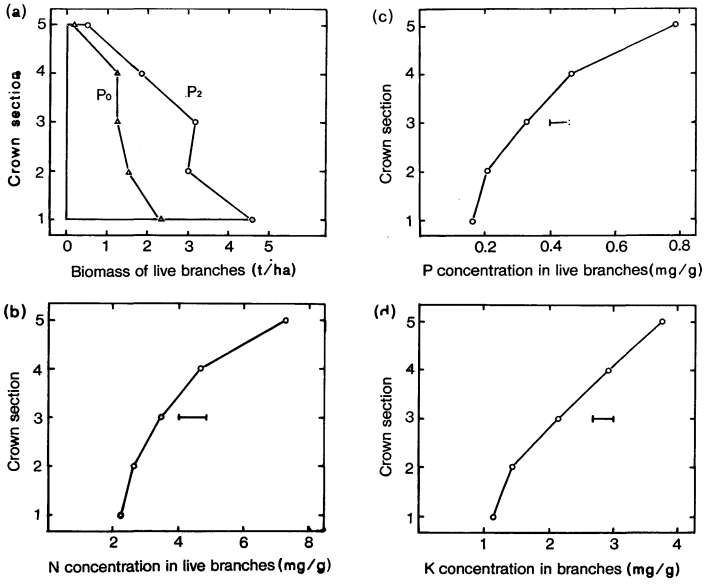

FIG. 3—Biomass (a) and the concentrations of nitrogen (b), phosphorus (c), and potassium (d) in the live branches of **P. radiata** aged 10 years by section of the green crown. Treatment effects were not significant for concentration so these data have been combined.

Nutrient concentrations in stem bark and stem wood were determined on only three discs in each tree and analysis of variance (Table 2) again showed no effect of treatment but a significant effect of section on all nutrients ($p < 0.001$). Ten discs from each sample tree had been used for the determination of dry weight of stem bark and stem wood biomass however, so these were all used in the analysis of variance. Both section and the section by treatment interaction were significant ($p < 0.01$) and the effect of treatment was significant for stem wood biomass ($p < 0.05$, Table 2).

Stem wood and stem bark biomass are shown against tree height in Fig. 4. Nutrient concentrations in the bark (which included the live phloem) were of the same order as those in the live branches, but concentrations in the wood were an order of magnitude lower than this (Fig. 5a–c). Concentrations of nutrients in the outer rings of wood were significantly higher than concentrations in the inner rings (Fig. 5d).

Discs removed from 0.2, 0.5, and 0.8 of tree height did not represent an average of the stem bark and stem wood biomass in each third of the stem height (Fig. 4). For the purposes of calculating nutrient content of stem wood and stem bark (Table 3), the fraction of the stem bark and stem wood biomass in each third of the tree height was determined from the areas under the curves in Fig. 4.

Biomass and nutrient contents of all components on an area basis are summarised in Table 3. Above-ground biomass and phosphorus content of fertilised trees was approximately double that of unfertilised trees but the proportional increase in nitrogen and potassium was somewhat less than this.

Standing litter samples were removed from all plots so it was possible to test for both fertiliser type and rate in the analysis of variance. Fertiliser application significantly increased the mass and phosphorus concentration in standing litter ($p < 0.001$) and, although fertiliser "type" had no significant influence, fertiliser "rate" significantly influenced the level of increase (Table 4a).

The mass of standing litter increased from 9.1 to 13.2 t/ha and the concentration of phosphorus increased from 0.49 to 0.84 mg/g as the rate of application increased from P_0 to P_3 (Table 4b). Type of fertiliser had no significant effect on the mass or

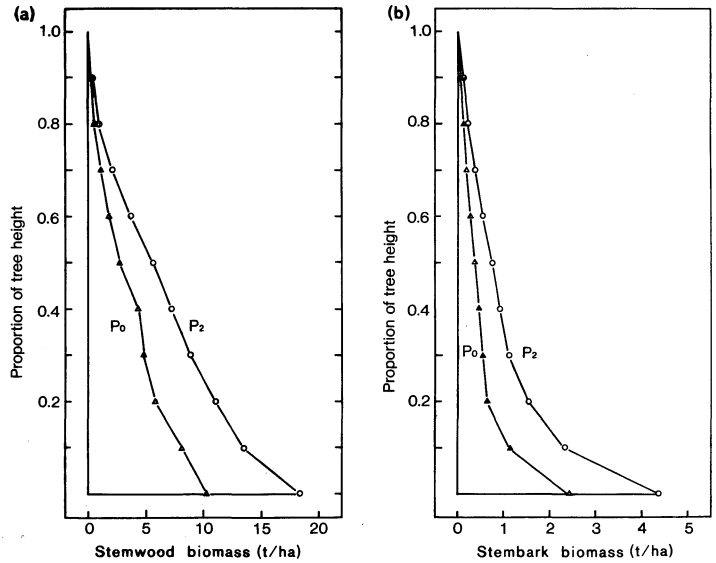

FIG. 4—Stem wood (a) and stem bark (b) biomass of unfertilised and fertilised **P. radiata** aged 10 years, over 10 sections of the stem.

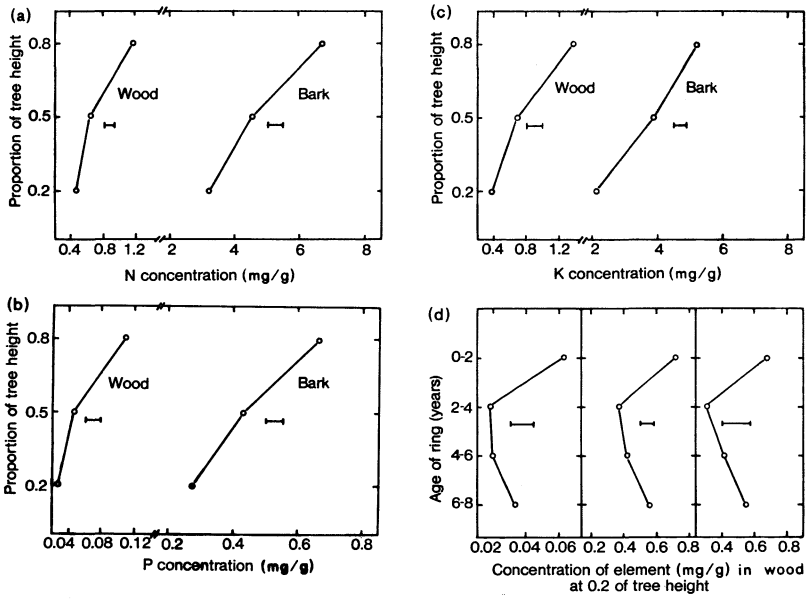

FIG. 5—Concentrations of nitrogen (a), phosphorus (b), and potassium (c) in the stem wood and stem bark of **P. radiata** aged 10 years. Data represent average values for points at 0.2, 0.5, and 0.8 of tree height. Elemental concentrations across the diameter of the discs from 0.2 of tree height are shown in (d).

TABLE 4—Mass and nutrients in standing litter under **P. radiata** aged 10 years

(a) Analysis of variance of mass and concentrations of nitrogen, phosphorus, and potassium

Factor	Mass	Nitrogen	Phosphorus	Potassium
Control **v.** Fertiliser	***	NS	***	NS
C **v.** Fert . Type	NS	NS	NS	NS
C **v.** Fert . Rate	*	NS	***	NS
C **v.** Fert . Rate . Type	NS	*	NS	NS

(b) Mass and nutrient concentration

Fertiliser rate	Mass (kg/ha)	Nutrient concentration (mg/g)		
		Nitrogen	Phosphorus	Potassium
P_0	9 100	9.09	0.49	0.84
P_1	10 800	8.82	0.51	0.83
P_2	12 120	8.84	0.58	0.85
P_3	13 200	9.10	0.84	0.85
LSD	1 750	—	0.06	—

NS Not significant
* $p < 0.05$
*** $p < 0.001$
LSD Least significant difference between two means ($p = 0.05$)

nutrient concentrations in the standing litter. Soil samples were also removed from all plots so the analysis of variance was the same as for standing litter. Fertiliser treatment significantly increased total nitrogen, extractable phosphorus (Bray No. 2), and cation exchange capacity, but decreased pH (Table 5). The most pronounced change was in extractable phosphorus and the rate of application had a significant ($p < 0.001$) effect on the level of this change. Whilst it was not possible to test for differences in extractable phosphorus with depth, the major changes occurred near the surface (Fig. 6).

TABLE 5—Analysis of variance table for soil characteristics in a **P. radiata** plantation aged 10 years. Average characteristics of unfertilised and all fertilised stands are also shown

Factor	pH	OM	N	P	K	CEC
C **v.** Fertiliser	*	NS	*	**	NS	**
C **v.** Fert . Type	NS	NS	NS	NS	NS	NS
C **v.** Fert . Rate	NS	NS	NS	***	NS	NS
C **v.** Fert . Type . Rate	NS	NS	NS	NS	NS	*
Control	5.53	2.05	0.043	1.27	0.039	3.06
Fertiliser	5.40	2.27	0.052	5.14	0.038	3.87

OM organic matter
N total nitrogen
P extractable phosphorus (Bray No. 2)
K exchangeable potassium
CEC cation exchange capacity
NS not significant
* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

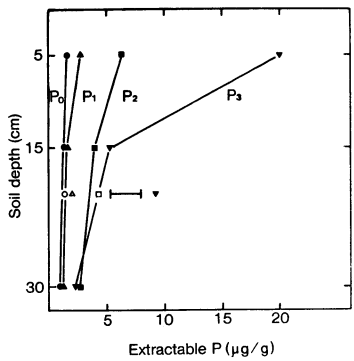

FIG. 6—Extractable soil phosphorus (Bray No. 2) at three depths from samples taken when the plantation was 10 years of age. Fertiliser was applied at three rates in the first 2 years after establishment. Open symbols represent mean values over the top 40 cm and LSD ($p = 0.05$) value applies to these.

The concentrations of phosphorus in the current needles of trees in the four phosphorus treatments over the 10 years of the experiment are shown in Fig. 7a. The concentrations in P_0 plots remained low throughout the period whereas those in P_3 plots remained high. Basal area growth for the same treatments over the period 4 to 10 years is shown in Fig. 7b and it can be seen that the differences in growth evident at age 10 had been established by age 4.

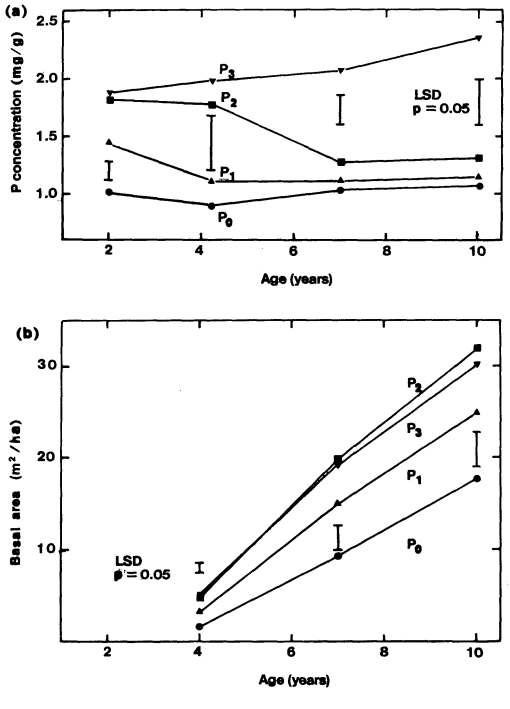

FIG. 7—(a) Phosphorus concentrations in the current needles of unfertilised and fertilised **P. radiata** between the ages of 2 and 10 years.
(b) Growth in basal area of fertilised and unfertilised **P. radiata** between the ages of 4 and 10 years.

DISCUSSION

There was a substantial response in growth to an application of 67 kg P/ha, which was reflected in all components of the above-ground biomass (Table 3). Despite this response to fertiliser, there were only minor differences in the way the biomass was distributed amongst the above-ground components in P_0 and P_2 plots. The major difference occurred in live needle biomass, which in P_2 plots represented only 9% of the total compared with 12.8% in P_0 plots. This difference was balanced by small increases in the proportions of stem wood, stem bark, and live branches in P_2 plots (Fig. 8).

Whilst the needle component represented a relatively small percentage of the total biomass, it contained by far the greatest percentage of the nitrogen in the biomass

with 56% in P_0 plots and 49% in P_2 plots. In P_2 plots, the needles contained 40% of the phosphorus but only 30% of the potassium (Fig. 8). Trees in P_0 plots contained slightly more of these three nutrients in their needles than P_2 plots.

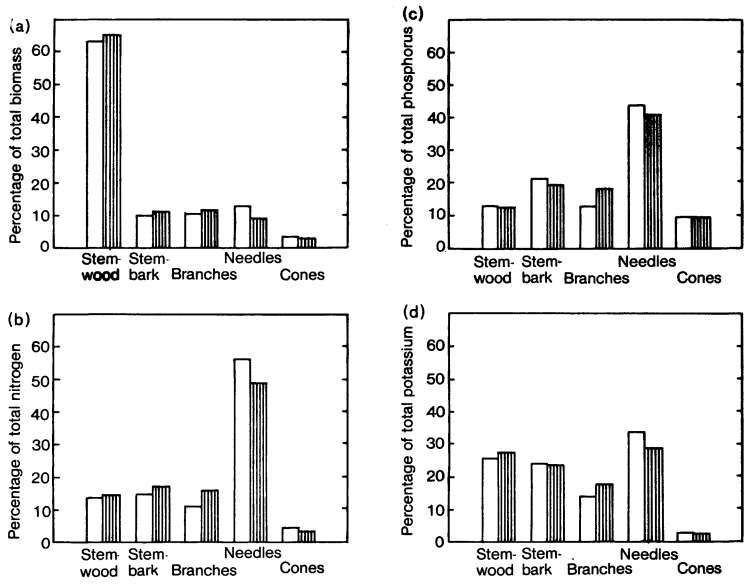

FIG. 8—The percentage of total above-ground biomass (a), nitrogen (b), phosphorus (c), and potassium (d) represented by the various components in unfertilised **P. radiata.**

The greatest percentage (66%) of the total biomass was contained in the stem wood but, whilst this component contained a relatively minor percentage of the nitrogen and phosphorus (14% and 13% respectively), it contained over 26% of the potassium. Studies in New Zealand have also demonstrated that *P. radiata* wood contains appreciable quantities of potassium (Orman & Will 1960; Will 1964; Madgwick *et al.* 1977). Severe potassium deficiency has occurred on similar soil types adjacent to the present experiment, generally after canopy closure (Hall & Raupach 1963). Potassium is normally considered a mobile element, but considerable quantities appear to be immobilised in the wood and bark, and on sites with low reserves this may ultimately lead to a deficiency in the needles.

The concentrations of nitrogen, phosphorus, and potassium in the needles were high at the top of the crown and decreased with height in the crown. There was also a decrease in the concentrations of nutrients as needles aged, but the influence of vertical position in the crown was more pronounced than the effect of age. Phosphorus concentrations in the current needles of about 1 mg/g indicate this element was severely deficient in the P_0 plots and the supply was apparently insufficient to permit large gradients in phosphorus concentration. The deficiency in P_2 plots was less severe and the

vertical gradient in phosphorus concentrations was steeper (Fig. 1b). An increase in root-absorbed phosphorus as a result of fertiliser application was also preferentially distributed to the growing points near the apex of the trees in the study by Flinn *et al.* (1982). Data from two *P. radiata* stands in South Australia indicated that greater temporal variation occurred in phosphorus concentration and content of needles from the more fertile of two sites (Fife & Nambiar 1982).

Similar data have been reported for potassium from a stand adjacent to the present study in which severely deficient trees had small vertical differences in potassium concentrations but fertilised trees had large gradients (Raupach 1967, and Fig. 2d). Whilst potassium concentrations in the needles of trees in the present experiment were low (Fig. 1c), those reported by Raupach (1967, and Fig. 2d) were considerably lower and potassium fertiliser applied to first-rotation trees in the experimental site apparently had some residual effect.

Differences in the concentrations of nutrients occur within plants and substantial re-distribution of nutrients occurs within the crowns of trees during the course of a year (e.g., Fife & Nambiar 1982). The reasons for such patterns have not been fully elucidated, but simulations using a biochemically based model of leaf photosynthesis enabled the distribution of leaf nitrogen for maximum carbon gain to be predicted over the canopy of an entire plant (Field 1983). It was concluded from this study that nitrogen re-distribution involved costs that were smaller than the benefits in increased photosynthesis. Results from this model (Field 1983) indicated that optimal nitrogen content increased with increasing daily photosynthetically active radiation, suggesting that high concentrations were of most benefit to leaves in the outer layers high in the crown.

A survey conducted by Turvey (1980) indicated that the mass of standing litter and the nutrient concentrations and contents in the litter reflected the differences in tree growth between groupings of similar soil types in Gippsland. In the present study, standing volume was not highly correlated with phosphorus in the standing litter or current foliage as plots fertilised at the P_2 and P_3 levels had similar growth but different concentrations of phosphorus in their foliage and litter. Merchantable volume at age 10, however, was highly correlated with the phosphorus concentration in the foliage at 2.5 years of age (variance accounted for = 65%). The concentration of phosphorus in the foliage at age 10 was highly correlated with concentration in the standing litter and exchangeable phosphorus in the top 10 cm of soil (variance accounted for = 74% and 68% respectively). A separate irrigation and fertiliser study on *P. radiata* also demonstrated there was a close relationship between nutrient concentrations in the current foliage and subsequent litter-fall (Cromer *et al.* 1984).

Highly significant relationships were observed between site productivity, foliar phosphorus levels, and exchangeable soil phosphorus (Bray No. 2 and Olsen) in 40-year-old *P. radiata* in New Zealand (Ballard 1970). Subsequent investigations showed that these tests could be used to predict early height growth and fertiliser requirements of *P. radiata* at time of planting in both New Zealand and Australia (Ballard 1974; Hopmans *et al.* 1978). The New Zealand work indicated that superphosphate requirements decreased from 170 g/seedling to nil as the extractable phosphorus in the top 10 cm of soil increased from 3 to 12 μg/g (Ballard 1974).

In Victoria, an application of 63 kg P/ha to a highly phosphorus-fixing soil resulted in approximately 5 μg/g of extractable phosphorus (Bray 2), whereas an application of 126 kg P/ha resulted in a value of approximately 15 μg/g over the top 10 cm (Flinn *et al.* 1982). In the present study, an extractable phosphorus concentration of 20 μg/g in P_3 plots and less than 6 μg/g in the top 10 cm of the remaining treatments (Fig. 6) indicates that, whilst the available phosphorus reserves had been depleted in P_2 plots, this did not reduce growth compared with P_3 plots and other factors must have been limiting.

The growth responses resulting from fertiliser application occurred at an early age (Fig. 7b, and Cromer *et al.* 1977) but were maintained to age 10 despite falling concentrations of phosphorus in the foliage of trees in P_1 and P_2 plots. In a fast-growing species such as *P. radiata,* cumulative growth reflects the historical rather than the current nutrient status. Plantations with adequate nutrient levels at establishment may not have sufficient reserves in the soil, which would subsequently lead to a dilution of nutrients in the tissues and possibly a reduction in growth rate.

A reduction in the concentration of a plant nutrient in the foliage has been referred to as the "dilution effect" in which additional growth induced by fertiliser can ultimately lead to lower nutrient concentrations in the foliage *(see* review by Jarrell & Beverly 1981). Ingestad (1982) has examined the effect in small seedlings and observed that a period of internal nutrient adjustment, or lag phase, occurs when the relative uptake rate of a particular nutrient falls below the relative growth rate of the plant. This concept is more difficult to visualise in large trees as the proportion of structural and storage tissue with low nutrient concentrations increases with age, and nutrient cycling becomes more important. However, the principle holds, that an increase in living biomass must be supported by an increase in nutrient mass or average nutrient concentrations will fall.

The three nutritional stages of a forest proposed by Miller (1981) are quite consistent with the theory put forward by Ingestad (1982) that relative growth rate is related to the relative addition rate of nutrients. During the years prior to canopy closure (Stage 1) growth is primarily dependent on soil nutrients, mineralisation of soil reserves may not keep pace with demand, and responses to applied nutrients can occur. It is likely that the changes in nutrient status shown in Fig. 7a are typical of stands established with fertiliser on nutrient-poor soils but there are few comparative data. The supply of exchangeable phosphorus (relative addition rate) fell below demand (relative growth rate) in P_1 plots after 2 years and growth rate declined to a level determined by the rate of supply of phosphorus. The relative addition rate of phosphorus in P_2 plots was equal to relative growth rate until age 4 years, after which it declined to a new steady state (Fig. 7a). The relative growth rate in P_3 plots was not limited by relative addition rate and phosphorus concentrations in the current foliage remained high.

The fact that growth rates in P_2 and P_3 plots did not differ after age 4 indicates that some factor other than phosphorus supply was limiting growth. Tree canopies in the heavily fertilised plots were virtually closed by age 4 and the factor most likely to have limited growth thereafter was water. Rainfall at the site averages approximately 700 mm per year and substantial increases in growth can result after irrigation of *P. radiata* on such sites (Cromer *et al.* 1983).

REFERENCES

BALLARD, R. 1970: The phosphate status of the soils of Riverhead Forest in relation to growth of radiata pine. **New Zealand Journal of Forestry 15:** 88–99.

——— 1974: Use of soil testing for predicting phosphate fertiliser requirements of radiata pine at time of planting. **New Zealand Journal of Forestry Science 4:** 27–34.

BRAY, R. H.; KURTZ, L. T. 1945: Determination of total, organic and available forms of phosphorus in soils. **Soil Science 59:** 39–45.

CRANE, W. B. J. 1981: Growth following fertilization of thinned **Pinus radiata** stands near Canberra in south-eastern Australia. **Australian Forestry 44:** 14–25.

CROMER, R. N.; TOMPKINS, D.; BARR, N. J. 1983: Irrigation of **Pinus radiata** with waste water: Tree growth in response to treatment. **Australian Forest Research 13:** 57–65.

CROMER, R. N.; BARR, N. J.; WILLIAMS, E. R.; McNAUGHT, A. M. 1985: Response to fertiliser in a **Pinus radiata** plantation. I: Above-ground biomass and wood density. **New Zealand Journal of Forestry Science 15:** 59–70.

CROMER, R. N.; DARGAVEL, J. B.; NELSON, P. F.; HENDERSON, V. T. 1977: More pulpwood from less land. **Appita 31:** 49–54.

CROMER, R. N.; TOMPKINS, D.; BARR, N. J.; WILLIAMS, E. R.; STEWART, H. T. L. 1984. Litter-fall in a **Pinus radiata** forest: The effect of irrigation and fertilizer treatments. **Journal of Applied Ecology 21:** 313–26.

DARGAVEL, J. B.; CROMER, R. N. 1979: Pulpwood, money and energy. **Australian Forestry 42**: 200–6.

FELLER, M. C. 1978: Nutrient movement into soils beneath eucalypt and exotic conifer forests in southern central Victoria. **Australian Journal of Ecology 3:** 357–72.

FIELD, C. 1983: Allocating leaf nitrogen for the maximization of carbon gain: Leaf age as a control on the allocation program. **Oecologia (Berlin) 56:** 341–7.

FIFE, D. N.; NAMBIAR, E. K. S. 1982: Accumulation and retranslocation of mineral nutrients in developing needles in relation to seasonal growth of young radiata pine trees. **Annals of Botany 50:** 817–29.

FLINN, D. W.; JAMES, J. M.; HOPMANS, P. 1982: Aspects of phosphorus cycling in radiata pine on a strongly phosphorus-adsorbing soil. **Australian Forest Research 12:** 19–35.

GENSTAT MANUAL 1977: "GENSTAT, A General Statistical Program". Numerical Algorithms Group Limited, Oxford.

HALL, M. J.; RAUPACH, M. 1963: Foliage analyses and growth responses in **Pinus radiata** (D. Don) showing potassium deficiencies in eastern Victoria. **Appita 17:** 76–84.

HOPMANS, P.; FLINN, D. W.; AEBERLI, B. C. 1978: Evaluation of soil testing methods for predicting early growth and responses to phosphatic fertilizer of **Pinus radiata** at Heywood, Victoria. **Australian Forest Research 8:** 57–61.

INGESTAD, T. 1982: Relative addition rate and external concentration: Driving variables used in plant nutrition research. **Plant, Cell and Environment 5:** 443–5.

JARRELL, W. M.; BEVERLY, R. B. 1981: The dilution effect in plant nutrition studies. **Advances in Agronomy 34:** 197–224.

KEEVES, A. 1966: Some evidence of loss of productivity with successive rotations of **Pinus radiata** in the south-east of South Australia. **Australian Forestry 30:** 51–63.

LOWTHER, J. R. 1980: Use of single sulphuric acid-hydrogen peroxide digest for the analysis of **Pinus radiata** needles. **Communications in Soil Science and Plant Analysis 11:** 175–88.

MADGWICK, H. A. I.; JACKSON, D. S.; KNIGHT, P. J. 1977: Above-ground dry matter, energy, and nutrient contents of trees in an age series of **Pinus radiata** plantations. **New Zealand Journal of Forestry Science 7:** 445–68.

MILLER, H. G. 1981: Forest fertilization: some guiding concepts. **Forestry 54:** 157–67.

ORMAN, H. R.; WILL, G. M. 1980: The nutrient content of **Pinus radiata** trees. **New Zealand Journal of Science 3:** 510–22.

RAUPACH, M. 1967: Soil and fertilizer requirements for forests of **Pinus radiata**. **Advances in Agronomy 19:** 307–53.

STACE, H. C. T.; HUBBLE, G. D.; BREWER, R.; NORTHCOTE, K. H.; SLEEMAN, J. R.; MULCAHY, M. J.; HALLSWORTH, E. G. 1972: "A Handbook of Australian Soils". Rellim, Adelaide, South Australia. 435 p.

STEWART, H. T. L.; FLINN, D. W.; JAMES, J. M. 1981: Biomass and nutrient distribution in radiata pine. **Proceedings, Australian Forest Nutrition Workshop, "Productivity in Perpetuity", Canberra:** 173–85.

TURVEY, N. D. 1980: A forest soil survey: II. The application of soil survey information to forestry operations. **Australian Forestry 43:** 172–7.

TURVEY, N. D.; POUTSMA, T. 1980: A forest soil survey: I. The provision of a factual soil framework for silvicultural management decisions. **Australian Forestry 43:** 165–71.

VEIHMEYER, T. J. 1929: An improved soil-sampling tube. **Soil Science 27:** 147–52.

WALKLEY, A.; BLACK, I. A. 1983: An examination of the Degtjareff method for the determination of soil organic matter. **Soil Science 37:** 29–38.

WARING, H. D. 1973: Early fertilization for maximum production. **Proceedings of FAO-IUFRO International Symposium on Forest Fertilization, Paris:** 215–41.

WILL, G. M. 1957: Variations in the mineral content of radiata pine needles with age and position in the crown. **New Zealand Journal of Science and Technology 38:** 699–706.

——— 1964: Dry matter production and nutrient uptake by **Pinus radiata** in New Zealand. **Commonwealth Forestry Review 43:** 57–70.

WOODS, R. V. 1980: An investigation into the relationship between fire and nutrient depletion leading to decline in productivity between rotations of **Pinus radiata** plantations in South Australia. **Woods and Forests Department, Miscellaneous Paper.** 55 p.