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Effect of spacing and age on nitrogen and phosphorus distribution in biomass of *Eucalyptus camaldulensis*, *Eucalyptus pellita* and *Eucalyptus urophylla* plantations in southeastern Brazil

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Abstract

The nitrogen and phosphorus accumulation in different tree parts (including root systems) of *Eucalyptus camaldulensis* Dehnh., *Eucalyptus urophylla* Blake and *Eucalyptus pellita* F. Muell. planted at three spacings (3 m × 1.5 m, 3 m × 3 m and 4 m × 3 m) and at three ages (15, 31 and 41 months) were evaluated in the savanna region of central Minas Gerais state in southeastern Brazil. A series of equations were produced to estimate per-tree nitrogen and phosphorus from age, spacing, diameter and height, and per-hectare nitrogen and phosphorus using age, spacing and a tally of tree diameters and heights. The highest N and P concentrations were observed in foliage (15–23 g N kg^{-1} and 0.8–1.1 g P kg^{-1}) and the lowest N concentration in bolewood (2.4–4.1 g N kg^{-1}), while the lowest P concentration was observed in the taproot (0.16–0.29 g P kg^{-1}). Total biomass N at age 41 months was greatest in *E. urophylla* (378–457 kg N ha^{-1}), lower in *E. pellita* (238–326 kg N ha^{-1}) and lowest in *E. camaldulensis* stands (204–240 kg N ha^{-1}), depending on spacing. Total biomass P at age 41 months was also greatest in *E. urophylla* (16.6–21.8 kg P ha^{-1}), and about equal in *E. pellita* (10.4–12.8 P ha^{-1}) and *E. camaldulensis* stands (10.4–12.2 kg P ha^{-1}), depending on spacing. As age and spacing increased, individual stems increased in diameter and total N and P, but the relationship between total N and P pools and age and spacing was more variable.

Keywords: Eucalyptus plantations; Nitrogen; Phosphorus; Tree spacing; Nutrient allocation

1. Introduction

Due to the requirement for more stringent environmental protection and changing economics of production, Brazil is increasingly looking to forest plantations for wood, fiber, energy and charcoal production. As a result, forest plantations in Brazil accounted for over 38% of industrial production while they occupied only 1.5% of forest land area in 1989, with more than half of the forest plantation area in Brazil devoted to *Eucalyptus spp.* plantations (Siqueira, 1989; Hakkila et al., 1992).

Further increases in total production from Brazilian plantation forests will come about in the future both by increasing the acreage of land devoted to forest plantations and also by increasing the per hectare

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productivity of those plantations where economical and possible. Increasing yield of wood products from existing forest plantations is very important for three reasons. First, increased production from plantation forests reduces the need for cutting of native forests (Anonymous, 1995), for which protection is highly desirable. Future standards for forest management, (i.e. ISO 14,001) will make worldwide marketing of wood cut from native forests nonrenewably and without consideration of environmental protection difficult. Second, additional productivity from existing forest plantations reduces the pressure for conversion of land from alternative uses, such as agriculture or native forest. Finally, when forest plantations are well located and managed, they can be more efficient and economical as sources of raw materials for Brazilian industry than native forests due to their proximity to Brazilian industry.

As the productivity of forest plantations is increased, however, the removal of N and P from those forests can also increase due to increased biomass removal. If N and P removals due to harvesting are increased beyond the level of demand of the new forest plantation for those nutrients, or beyond the forest ecosystem's ability to renew them through internal and external inputs, productivity may decrease over time due to nutrient depletion, and the goal of sustained or increased productivity per hectare not realized. In some cases, small changes in silvicultural or harvesting regimes may be sufficient to avoid N and P depletion completely. In other cases, N and P removed by harvest may be economically added. However, if the potential impacts of harvest removals of N and P are not assessed, reductions in site quality and forest productivity may take place without being recognized.

Any reductions in productivity due to N and P depletion will counteract any genetic and silvicultural improvements that are developed to increase productivity per unit land area, and must be avoided to insure the possibility of future productivity increases of Brazilian forest plantations. The first step in assessing the effects of harvest removals on N and P availability is to determine the location of nutrients in the trees. This should be done under a range of silvicultural techniques (i.e. species, spacing, management, harvest age and harvest intensity), that are likely to be utilized in actual management.

The second step is to assess potential removals in comparison to biomass or ecosystem pools. Ideally, the effects of N and P removals would be assessed by following the growth of subsequent stands, with an extreme removal rate above those normally utilized to assess extreme conditions. However, we know of no such studies that have been initiated in Brazil. This paper represents an effort to assess the location of N and P in *Eucalyptus* trees and potential removals due to harvesting. The potential effects of age and spacing on accumulation and harvest removals of N and P are measured for *E. camaldulensis*, *E. pellita* and *E. urophylla* forest plantations in the Cerrado region of Minas Gerais State in southeastern Brazil.

2. Methods and materials

2.1. Study location, design and determination of biomass

This study was carried out on Pains Corporation plantations established near the city of Três Marias in central Minas Gerais state (18°13.1′S by 45°08.3′W). Characteristics of the site include nearly level land (0–2% slope), an altitude of 539 m, an annual mean temperature of 21°C, an annual precipitation from 1100 to 1420 mm, and an estimated hydraulic deficit of 60 mm (Bernardo, 1995). Plantations were established in January, 1989 following site clearing and bedding. A company standard application of 11 kg ha^{-1} of total nitrogen, 175 kg ha^{-1} of total phosphorus, 5.5 kg ha^{-1} of total potassium and 90 kg ha^{-1} of total sulfur were applied at planting.

The experiment consists of three repetitions of two treatments, including treatments of spacing (3 m × 1.5 m, 3 m × 3 m and 4 m × 3 m) and species (*E. camaldulensis, E. pellita*, and *E. urophylla*). Study plots were laid out using a treatment area of 9 × 9 trees with a growth measurement area of 5 × 5 trees and a two-row buffer around the growth measurement area. Details of the study design are given in Bernardo (1995).

A total of 81 trees representing a range of diameters and heights were selected for measurement and nutrient analysis to develop biometrical estimation equations. Tree parts sampled included bolewood, bole bark, branches, foliage, taproot, lateral roots >2 mm and lateral roots <2 mm (Bernardo, 1995). Equations for biomass estimation of per hectare pools of bole wood, bole bark, branches, foliage, taproots, roots >2 mm and roots <2 mm were generated by calculating linear regression estimates of dry mass using diameter, total height, stand age and spacing as predictors. Dry mass for each tree was calculated by multiplying diameter, total height, spacing and age of each live tree measured in each treatment plot individually by estimation equations (Bernardo, 1995).

2.2. Nutrient analysis and calculation of nutrient pools

All samples were prepared by grinding, dried to 85°C to constant mass and analyzed for total N and P. A separate study showed that drying to 85°C was not significantly different than drying to 105°C. Total N was measured by Kjeldahl digestion (Bremner and Mulvaney, 1982) and total P by acid digestion and determination of phosphate by molybdate reduction. Nutrient pools were calculated by multiplying nutrient concentrations of tree parts by the total biomass of each tree part as estimated above. This gave an estimate of total N or P per hectare for seven tree parts (bole wood, bole bark, branches, foliage, taproots, roots >2 mm and roots <2 mm), three species (*E. camaldulensis, E. pellita*, and *E. urophylla*), three spacings (3 m × 1.5 m, 3 m × 3 m and 4 m × 3 m), three ages (15, 31 and 41 months), and three repetitions (Bernardo, 1995).

The effect of plantation spacing and species on N and P concentrations and contents at age 15, 31 and 41 months was tested using ANOVA with a Tukey comparison of means (0.05 level) as an ad hoc test (SYSTAT, 1990).

3. Results and discussion

3.1. Elemental concentrations of tree parts

3.1.1. Comparison of tree parts

The concentrations of N and P varied greatly between different tree parts, with foliage having the highest concentration (Table 1). This corresponds well with other studies of nutrient contents of forests in

Table 1
Average total N and P concentrations for tree parts

Nutrient	Tree part	*Eucalyptus camaldulensis*		*Eucalyptus pellita*		*Eucalyptus urophylla*	
		Concentration[a]	SD[b]	Concentration[a]	SD[b]	Concentration[a]	SD[b]
N (g N kg^{-1})							
	Foliage	23.2 cA	(5.9)	15.7 cA	(4.6)	21.1 bA	(6.8)
	Branches	5.3 bA	(2.2)	4.2 abA	(1.8)	6.1 aA	(2.6)
	Bole bark	4.9 bA	(1.6)	5.0 abA	(1.7)	5.6 aA	(1.8)
	Bolewood	2.4 aA	(1.0)	3.8 aA	(1.3)	4.1 aA	(3.2)
	Taproot	3.9 bA	(0.9)	5.8 abB	(1.5)	5.6 aAB	(3.0)
	Roots >2 mm	4.8 bA	(1.9)	5.3 abA	(1.5)	5.6 aA	(1.6)
	Roots <2 mm	6.3 bA	(1.8)	7.0 bA	(1.9)	5.7 aA	(1.3)
P (g P kg^{-1})							
	Foliage	1.08 cA	(0.25)	0.80 cA	(0.18)	1.01 cA	(0.19)
	Branches	0.41 bA	(0.21)	0.27 abA	(0.14)	0.44 bA	(0.20)
	Bole bark	0.61 bB	(0.33)	0.32 abA	(0.09)	0.69 bB	(0.26)
	Bolewood	0.28 abA	(0.17)	0.20 aA	(0.09)	0.18 aA	(0.09)
	Taproot	0.16 aA	(0.07)	0.29 abB	(0.11)	0.20 aAB	(0.10)
	Roots >2 mm	0.19 aA	(0.06)	0.25 aA	(0.06)	0.24 aA	(0.08)
	Roots <2 mm	0.37 bA	(0.16)	0.40 bA	(0.12)	0.29 abA	(0.08)

[a] Mean differences tested with a Tukey ANOVA (0.05 level); small letters indicate differences in means by spacing only among individual tree parts; capital letters indicate differences in means by species only among individual tree parts.
[b] Figures in parentheses represent standard deviations of the mean values.

general (Boerner, 1984; Pereira et al., 1984; Poggiani et al., 1983; Timmer and Morrow, 1984; Hopmans et al., 1993) and the recognized high biological activity of foliage (Mengel and Kirkby, 1982). In general, the concentrations for N varied as foliage > branches, bole bark, roots > bolewood. The concentration of P varied as foliage > branches, bole bark, small roots > taproot, coarse roots, bolewood.

The concentration of P in foliage was somewhat lower than in another study that looked at nutrients in seedlings. For instance, in *E. camaldulensis* total P was 1.08 vs. 1.80 mg kg^{-1} in this study vs. the study of Borges (1986). In *E. urophylla* total foliar P was 1.0 vs. 0.6 mg kg^{-1} (Neves et al., 1986). The critical levels of nutrients for *E. camaldulensis* and *E. urophylla* are not well established, so it cannot be predicted if these stands are nutrient deficient at these concentrations.

Data from another study of *E. urophylla* near Ipatinga, Minas Gerais (Reis and Barros, 1990) shows somewhat different concentrations for the bole compared to this study. For instance, the nutrient concentrations in this study vs. the study of Reis and Barros (1990) for the bole (bolewood + bole bark) were 3.1 vs. 1.8 mg kg^{-1} for N and 0.16 vs. 0.29 mg kg^{-1} for P.

In general, the concentration of most nutrients analyzed in tree parts decreased with increasing age (Table 2). Notably, foliage showed a slight increase in N concentration with time. The taproot showed the smallest relative changes in N and P concentration with time overall. This has been observed in other studies (Bellote et al., 1980; DeBell and Radwan, 1984; Vogt et al., 1987). The highest reductions in N and P concentrations with time were in bolewood, which showed an average reduction of 34% for N and 65% for P (both significant at 0.05 level) from age 15 to 41 months. Other tree parts were variable in N and P concentration changes with time (Table 2).

As spacing was increased, N and P concentrations in the various tree parts increased, though not greatly except in the bolewood and taproots (Table 3), probably due to decreased competition for N and P with increased spacing (Ostman and Weaver, 1982; Hager and Kazda, 1985). This will tend to counteract the concept of increasing nutrient conservation by growing trees to larger individual dimensions at increased spacing. However, the effect was relatively small compared to the effect of age or the potential shifting of additional material onto bolewood vs. bole bark or branches. Despite the observation of an overall increase in average nutrient concentration with increased spacing, there were significant changes only for bolewood N, which increased 53% in N concentration, taproot P (43%) and P in roots <2 mm (22%). Most changes were small and not statistically significant.

Table 2
Percent reduction in average nutrient concentrations with increased age from 15 to 41 months

Tree part	N		P	
	Concentration[a]	SD[b]	Concentration[a]	SD[b]
Foliage	−5	(37)	19*	(17)
Branches	29*	(31)	32*	(34)
Bole bark	11	(65)	15	(57)
Bolewood	34*	(25)	65*	(15)
Taproot	3	(35)	11	(45)
Roots >2 mm	6	(39)	27*	(26)
Roots <2 mm	25*	(18)	40*	(20)

[a] A '*' signifies that the confidence interval (0.05 level) of the mean does not include a value of 0 (a significant change in concentration). A positive value represents a decrease in nutrient concentration, and a negative value an increase in average nutrient concentration as age is increased from 15 to 41 months.

[b] Figures in parentheses represent standard deviations of the mean values.

Table 3
Percent increase in average nutrient concentrations of tree parts spacing from 3 × 1.5 m to 4 × 3 m

Tree part	N		P	
	Concentration[a]	SD[b]	Concentration[a]	SD[b]
Foliage	7	(63)	−4	(24)
Branches	3	(45)	34	(98)
Bole bark	2	(36)	18	(51)
Bolewood	53*	(111)	18	(52)
Taproot	28	(99)	43*	(99)
Roots >2 mm	10	(42)	14	(39)
Roots <2 mm	5	(28)	22*	(51)

[a] A '*' signifies that the confidence interval (0.05 level) of the mean does not include a value of 0 (a significant change in concentration). A positive value represents an increase in nutrient concentration, and a negative value a decrease in average nutrient concentration as spacing is increased from 3 × 1.5 m to 4 × 3 m.

[b] Figures in parentheses represent standard deviations of the mean values.

3.1.2. Effect of species

There were relatively small differences in N and P concentrations for individual tree parts among species (Table 1). However, the concentration of P in bole bark was significantly (0.05 level) greater in *E. camaldulensis* (0.61 g kg^{-1}) and *E. urophylla* (0.69 g kg^{-1}) than in *E. pellita* (0.32 g kg^{-1}). The concentration of P in the taproot was greater in *E. pellita* (0.29 g kg^{-1}) than in *E. camaldulensis* (0.16 g kg^{-1}).

3.2. Nitrogen pools of trees

3.2.1. Effect of species

There was a significant effect of species on the N content of some tree parts (Table 4). The root system overall showed the lowest CV among species (14%), while the roots <2 mm in diameter showed the highest (96%), with a 35% CV for the whole tree (roots + above-ground). In most cases, N was of the order *E. urophylla* > *E. camaldulensis*, *E. pellita.*

Table 4
Total per area N for each tree part by species and spacing at 41 months

Tree part		*Eucalyptus camaldulensis*		*Eucalyptus pellita*		*Eucalyptus urophylla*	
		Total N[a]	SD[b]	Total N[a]	SD[b]	Total N[a]	SD[b]
	(kg N ha^{-1})						
Foliage	3 m × 1.5 m	93 aA	(36)	118 a AB	(54)	224 aB	(49)
	3 m × 3 m	84 aA	(21)	83 aA	(28)	171 aB	(34)
	4 m × 3 m	66 aA	(23)	89 aA	(21)	198 aB	(65)
Branches	3 m × 1.5 m	35 bA	(8)	22 aA	(5)	38 aA	(14)
	3 m × 3 m	21 ab A	(7)	18 aA	(8)	40 aB	(7)
	4 m × 3 m	18 aA	(7)	14 aA	(4)	33 aB	(12)
Bole bark	3 m × 1.5 m	12 aA	(6)	17 aA	(2)	20 aA	(5)
	3 m × 3 m	9 aA	(2)	24 aA	(11)	17 aA	(5)
	4 m × 3 m	9 aA	(1)	11 aA	(3)	15 aA	(6)
Bole wood	3 m × 1.5 m	33 aA	(6)	49 aA	(13)	89 aB	(6)
	3 m × 3 m	20 aA	(5)	40 a AB	(21)	68 aB	(22)
	4 m × 3 m	26 aA	(12)	39 a AB	(10)	88 aB	(35)
Taproot	3 m × 1.5 m	28 aA	(8)	54 aB	(7)	36 aA	(7)
	3 m × 3 m	24 aA	(2)	38 aA	(2)	28 aA	(12)
	4 m × 3 m	20 aA	(2)	38 aA	(15)	22 aA	(7)
Lateral roots >2 mm diameter	3 m × 1.5 m	29 aB	(8)	56 aC	(8)	7 aA	(1)
	3 m × 3 m	43 aA	(23)	43 aA	(16)	10 ab A	(5)
	4 m × 3 m	53 aB	(26)	37 a AB	(13)	16 bA	(4)
Lateral roots <2 mm diameter	3 m × 1.5 m	10 aA	(1)	9 aA	(3)	42 aB	(10)
	3 m × 3 m	9 aA	(2)	9 aA	(1)	45 aB	(7)
	4 m × 3 m	12 aA	(3)	9 aA	(3)	52 aB	(6)
Above-ground	3 m × 1.5 m	173 aA	(53)	206 aA	(68)	372 aB	(46)
	3 m × 3 m	134 aA	(14)	165 aA	(12)	295 aB	(40)
	4 m × 3 m	120 aA	(25)	153 aA	(22)	335 aB	(104)
Below-ground	3 m × 1.5 m	67 aA	(12)	120 aB	(10)	85 aA	(16)
	3 m × 3 m	76 aA	(25)	90 aA	(15)	83 aA	(9)
	4 m × 3 m	85 aA	(31)	85 aA	(29)	91 aA	(16)
Total tree	3 m × 1.5 m	240 aA	(65)	326 a AB	(78)	457 aB	(46)
	3 m × 3 m	210 aA	(30)	254 aA	(3)	378 aB	(46)
	4 m × 3 m	240 aA	(7)	238 aA	(51)	426 aB	(119)

[a] Mean differences tested with a Tukey ANOVA (0.05 level); small letters indicate differences in means by spacing only among individual tree parts; capital letters indicate differences in means by species only among individual tree parts.

[b] Figures in parentheses represent standard deviations of the mean values.

Total N in the whole tree (above-ground + below-ground; average of three spacings) was 218 kg ha^{-1} for *E. camaldulensis*, compared to 273 kg ha^{-1} for *E. pellita* and 420 kg ha^{-1} for *E. urophylla*. The above-ground total N pool was 142 kg ha^{-1} for *E. camaldulensis*, while *E. pellita* was 175 kg ha^{-1} and *E. urophylla* was 334 kg ha^{-1}. The root system held substantial N, an average of 76 kg ha^{-1} for *E. camaldulensis*, 98 kg ha^{-1} for *E. pellita*, and 86 kg ha^{-1} for *E. urophylla*. The foliage, though it represented a rather small amount of the total biomass (Bernardo et al., 1997) represented much more of the total N pool, 37% for *E. camaldulensis*, 35% for *E. pellita* and 47% for *E. urophylla*.

Compared to the large amount of biomass in bole material, an average of 49% for *E. urophylla*, 46% for *E. urophylla*, and 50% for *E. urophylla* at 41 months (Bernardo et al., 1997), the bolewood was a fairly small component of total N. For instance, only 12% of total N was in the bole for *E. camaldulensis*, 16% for *E. pellita* and 19% for *E. urophylla*. If a harvest regime removed the entire bole (bolewood + bole bark), the removal would be 17% of total tree N for *E. camaldulensis*, 22% for *E. pellita*, and 24% for *E. urophylla*. In the event that the entire above-ground component of a stand is harvested (or moved to another location due to remote debranching), the loss of total N accumulated in vegetation would be much greater at 65% for *E. urophylla*, 64% for *E. pellita*, and 79% for *E. urophylla*, a very large proportion of total tree N.

3.2.2. Effect of spacing

The spacing at which seedlings were planted had an effect on absolute amounts of N in biomass per hectare (Table 4). For instance, increasing spacing from 3 × 1.5 m to 4 × 3 m reduced total N (above-ground + roots) by 15% in *E. camaldulensis*, 27% in *E. pellita*, and 7% in *E. urophylla* (Table 4 and Fig. 1). Increasing spacing from 3 × 1.5 m to 4 × 3 m reduced the above-ground total N by 31% in *E. camaldulensis*, 25% in *E. pellita*, and 10% in *E. urophylla*, reduced root system biomass N by 26% in *E. camaldulensis* and 6% in *E. urophylla,*and increased root system biomass by 29% in *E. pellita* (Table 4 and Fig. 1).

The distribution of N among specific tree parts was also changed with spacing changes, with most tree parts showing decreased total N per hectare with

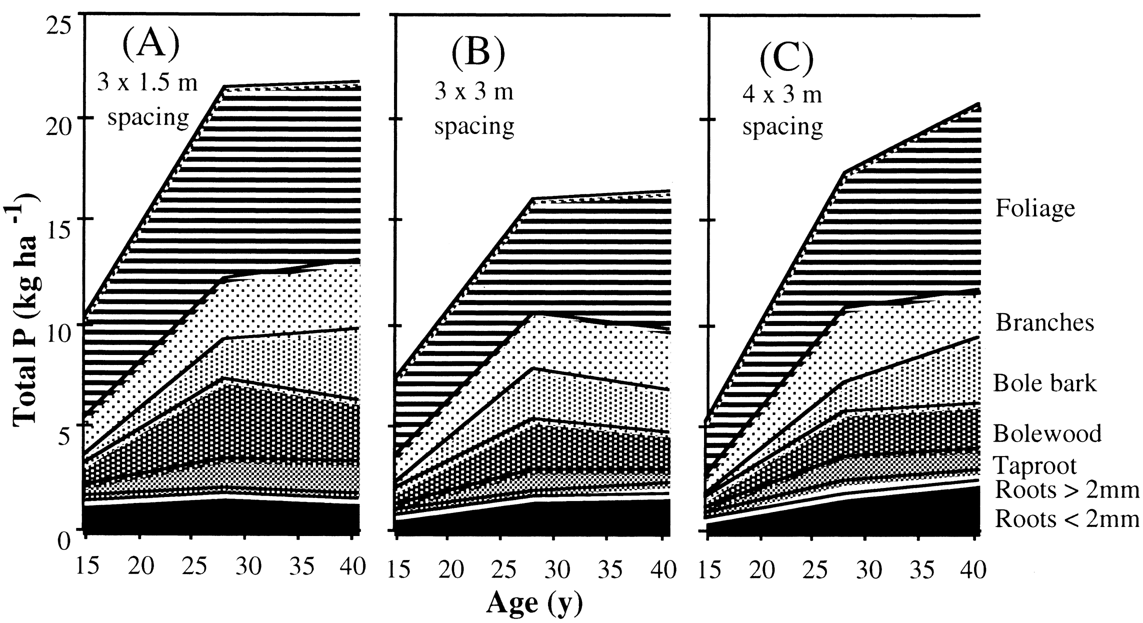

Fig. 1. Average per hectare total N pools of tree parts vs. age for *E. urophylla* at (A) 3 m × 1.5 m, (B) 3 m × 3 m and (C) 4 m × 3 m spacing levels.

increased spacing. For instance, the amount of foliage N per hectare decreased by 29% in *E. camaldulensis*, 24% in *E. pellita*, and 11% in *E. urophylla*. The amount of bolewood N per hectare decreased by 21% in *E. camaldulensis*, 20% in *E. pellita*, and 1% in *E. urophylla*. The total amount of N in branches decreased by 48% in *E. camaldulensis*, 36% in *E. pellita*, and 13% in *E. urophylla*.

Spacing also had effects on relative allocation to the root system. For instance, the root : shoot N ratio (total above-ground N vs. total below-ground N) changed from 0.39 to 0.71 for *E. camaldulensis*, but was relatively unchanged at 0.58 to 0.55 for *E. pellita*, and 0.23 to 0.27 for *E. urophylla*, as spacing was increased from 3 × 1.5 m to 4 × 3 m. The fine root : -coarse root ratio changed from 0.36 to 0.22 for *E. camaldulensis*, 0.17 to 0.25 for *E. pellita*, and 6.0 to 3.2 for *E. urophylla*, as spacing was increased from 3 × 1.5 m to 4 × 3 m.

3.2.3. Effect of age

As expected, age had a significant effect on biomass N. The weights of most tree parts increased substantially with age (Bernardo et al., 1997), and so did the average total N per hectare (Fig. 1). However, the decrease in average nutrient concentrations of tree parts with age (Table 2) offsets some of the increase in raw biomass, and the net result is increased nutrient efficiencies with increased age. For instance, Table 5 shows the percent increase in nutrient efficiency (average of all 27 plots) for individual tree parts from age 15 to 41 months. The increase in efficiency is 58% the bole (wood + bark) and 65% for the whole tree. All tree parts except for foliage show significant increases in biomass production for N utilized.

The effect of age on total N was also somewhat different at each spacing level. For instance, in *E. urophylla* (*E. camaldulensis* and *E. pellita* are similar), total N is higher at 15 months for most tree parts in the 3 m × 1.5 m spacing level, indicating a quicker occupancy of the site and quicker accumulation of biomass and nutrients. However, by the end of 41 months the differences in total N are very small (Fig. 1). The largest fraction of total N is in the foliage at all ages. Though total biomass is relatively greater than total N at the 3 × 1.5 m vs. 4 × 3 m spacing level (Bernardo et al., 1997), increases in nutrient concentration with increased spacing level (Table 3) accounts for much of the lack of differences observed. This reflects observations of growth vs. spacing in Australia (Binkley et al., 1997: Cromer et al., 1993).

3.3. Phosphorus pools of trees

3.3.1. Effect of species

There was a significant effect of species on the P content of some tree parts. The root system showed the lowest coefficient of variation (17%), while the roots

Table 5
Percent increase in average nutrient efficiency with increased age from 15 to 41 months

Tree part	N		P	
	Efficiency[a]	SD[b]	Efficiency[a]	SD[b]
Foliage	7	(36)	28*	(26)
Branches	69*	(71)	83*	(91)
Bole bark	37*	(45)	82*	(138)
Bolewood	70*	(65)	241*	(163)
Taproot	16*	(41)	41*	(68)
Roots >2 mm	23*	(45)	52*	(53)
Roots <2 mm	45*	(49)	84*	(62)
Bole (wood + bark)	58 *	(47)	171*	(153)
Above-ground	97*	(63)	136*	(64)
Below-ground	26*	(29)	64*	(50)
Whole tree	65*	(39)	103*	(49)

[a] Where nutrient efficiency is defined as dry weight/total nutrient (per hectare). A '*' signifies that the confidence interval (0.05 level) of the mean does not include a value of 0 (a significant change in efficiency). A positive value represents an increase in nutrient efficiency and a negative value a decrease in nutrient efficiency as spacing is increased from 3 × 1.5 m to 4 ×3 m.

[b] Figures in parentheses represent standard deviations of the mean values.

<2 mm in diameter showed the highest (87%), with a 34% C.V. for the whole tree (roots + above-ground). In most cases, total P was of the order *E. urophylla* > *E. camaldulensis*, *E. pellita*.

Total P in the whole tree was 11.0 kg ha^{-1} for *E. camaldulensis*, compared to 11.7 kg ha^{-1} for *E. pellita* and 19.7 kg ha^{-1} for *E. urophylla*. The above-ground total P pool was 8.0 kg ha^{-1} for *E. camaldulensis*, while *E. pellita* was 7.5 kg ha^{-1} and *E. urophylla* was 16.2 kg ha^{-1}. The root system had an average of 3.0 kg ha^{-1} for *E. camaldulensis*, 4.2 for *E. pellita*, and 3.5 for *E. urophylla*. The foliage, though it represented a rather small amount of the total biomass (Bernardo et al., 1997) represented much more of the P pool, a total of 31% for *E. camaldulensis*, 35% for *E. pellita* and 41% for *E. urophylla*.

Compared to the large proportion of total biomass in bolewood, the total P in bolewood was a fairly small fraction, 21% for *E. camaldulensis*, 12% for *E. pellita* and 12% for *E. urophylla*. If a harvest regime removed the entire bole (bolewood + bole bark), the removal would be 29% of total tree P for *E. camaldulensis*, 20% for *E. pellita*, and 26% for *E. urophylla*. In the

Table 6
Total per area P for each tree part by species and spacing at 41 months

Tree part		*Eucalyptus camaldulensis*		*Eucalyptus pellita*		*Eucalyptus urophylla*	
		Total P[a]	SD[b]	Total P[a]	SD[b]	Total P[a]	SD[b]
	(kg P ha^{-1})						
Foliage	3 m × 1.5 m	4.0 aA	(0.8)	4.4 aA	(1.1)	8.5 aB	(1.4)
	3 × m 3 m	3.6 aA	(0.6)	3.7 aA	(1.1)	6.8 aB	(1.6)
	4 m × 3 m	2.8 aA	(0.8)	4.1 aA	(1.0)	9.1 aB	(1.0)
Branches	3 m × 1.5 m	1.7 aA	(0.6)	1.1 aA	(0.4)	3.4 aA	(2.3)
	3 m × 3 m	1.4 aA	(0.2)	0.9 aA	(0.5)	3.0 aB	(0.2)
	4 m × 3 m	1.1 aA	(0.7)	1.3 aA	(0.6)	2.4 aA	(0.4)
Bole bark	3 m × 1.5 m	0.9 aA	(0.5)	0.9 aA	(0.3)	3.5 aB	(1.8)
	3 m × 3 m	0.6 aA	(0.1)	1.0 aA	(0.4)	2.0 aB	(0.4)
	4 m × 3 m	1.0 aA	(0.2)	0.8 aA	(0.4)	3.1 aB	(0.7)
Bole wood	3 m × 1.5 m	3.1 aA	(2.0)	1.6 aA	(0.4)	3.0 aA	(1.0)
	3 m × 3 m	1.9 aA	(0.7)	1.3 aA	(0.4)	1.8 aA	(0.4)
	4 m × 3 m	2.0 aA	(0.1)	1.4 aA	(0.2)	2.1 aA	(0.6)
Taproot	3 m × 1.5 m	1.1 aA	(0.3)	2.0 aA	(1.3)	1.5 aA	(0.4)
	3 m × 3 m	1.0 aA	(0.9)	1.2 aA	(0.2)	0.8 aA	(0.2)
	4 m × 3 m	0.9 aA	(0.3)	1.9 aA	(0.7)	1.1 aA	(0.3)
Lateral roots >2 mm diameter	3 m × 1.5 m	1.1 aA	(0.1)	2.4 aB	(0.7)	0.3 aA	(0.0)
	3 m × 3 m	1.6 aB	(0.9)	1.8 aB	(0.1)	0.4 ab A	(0.1)
	4 m × 3 m	2.0 aB	(0.3)	2.0 aB	(1.0)	0.6 cA	(0.1)
Lateral roots<2 mm diameter	3 m × 1.5 m	0.4 aA	(0.1)	0.4 aA	(0.1)	1.6 aB	(0.2)
	3 m × 3 m	0.4 aA	(0.1)	0.5 aA	(0.1)	1.8 aB	(0.2)
	4 m × 3 m	0.6 bA	(0.1)	0.6 aA	(0.1)	2.4 aB	(0.6)
Above-ground	3 m × 1.5 m	9.6 a AB	(3.7)	7.9 aA	(2.1)	18.4 aB	(4.9)
	3 m × 3 m	7.5 aA	(1.5)	6.9 aA	(1.1)	13.6 aB	(2.1)
	4 m × 3 m	6.9 aA	(1.5)	7.5 aA	(1.8)	16.7 aB	(2.2)
Below-ground	3 m × 1.5 m	2.6 aA	(0.2)	4.8 aA	(2.0)	3.4 aA	(0.4)
	3 m × 3 m	3.0 aA	(1.8)	3.5 aA	(0.5)	3.0 aA	(0.5)
	4 m × 3 m	3.5 aA	(0.6)	4.4 aA	(1.6)	4.1 aA	(0.9)
Total tree	3 m × 1.5 m	12.2 aA	(3.8)	12.8 aA	(3.8)	21.8 aA	(5.1)
	3 m × 3 m	10.5 aA	(3.3)	10.4 aA	(1.6)	16.6 aB	(2.0)
	4 m × 3 m	10.4 aA	(0.9)	12.0 aA	(2.8)	20.8 aB	(3.2)

[a] Mean differences tested with a Tukey ANOVA (0.05 level); small letters indicate differences in means by spacing only among individual tree parts; capital letters indicate differences in means species only among individual tree parts.

[b] Figures in parentheses represent standard deviations of the mean values.

event that the entire above-ground component of a stand is harvested (or moved), the loss of total P accumulated in vegetation would be 72% for *E. urophylla*, 64% for *E. pellita*, and 82% for *E. urophylla*, which constitutes the bulk of total tree P.

3.3.2. Effect of spacing

The spacing at which seedlings were planted had an effect on absolute amounts of P in biomass per hectare. For instance, increasing spacing from 3 × 1.5 m to 4 × 3 m reduced total P (above-ground + roots) by 15% in *E. camaldulensis*, 6% in *E. pellita*, and 4% in *E. urophylla* (Table 6 and Fig. 2). Increasing spacing from 3 × 1.5 m to 4 × 3 m reduced the above-ground total P by 29% in *E. camaldulensis*, 5% in *E. pellita*, and 9% in *E. urophylla*. Root system biomass P decreased by 35% in *E. camaldulensis* and 22% in *E. urophylla*, and increased by 8% in *E. pellita* (Table 6 and Fig. 2).

The distribution of P among specific tree parts was also changed with spacing changes, with most tree parts showing decreased total P with increased spacing. For instance, the amount of foliage P per hectare decreased by 30% in *E. camaldulensis*, 7% in *E. pellita*, and increased by 7% in *E. urophylla*. The amount of bolewood P per hectare decreased by 34% in *E. camaldulensis*, 10% in *E. pellita*, and 29% in *E. urophylla*. The total amount of P in branches decreased by 35% in *E. camaldulensis*, 30% in *E. urophylla* and increased by 13% in *E. pellita*.

Spacing also had effects on relative allocation of P to the root system. For instance, the root : shoot P ratio (total above-ground P vs. total below-ground P) changed from 0.27 to 0.51 for *E. camaldulensis*, and 0.18 to 0.24 for *E. urophylla*; however, it was relatively unchanged from 0.61 to 0.59 for *E. pellita* as spacing was increased from 3 × 1.5 m to 4 × 3 m. The fine root : coarse root ratio decreased from 0.37 to 0.31 for *E. camaldulensis*, 6.1 to 4.2 for *E. urophylla*, and increased from 0.18 to 0.28 for *E. pellita*, as spacing was increased from 3 × 1.5 m to 4 × 3 m.

3.3.3. Effect of age

The average total P per hectare increased substantially with stand age (Fig. 2). However, the decrease in average nutrient concentrations of tree parts with age (Table 2) and increased allocation to the stem increases nutrient efficiency with age, so that the

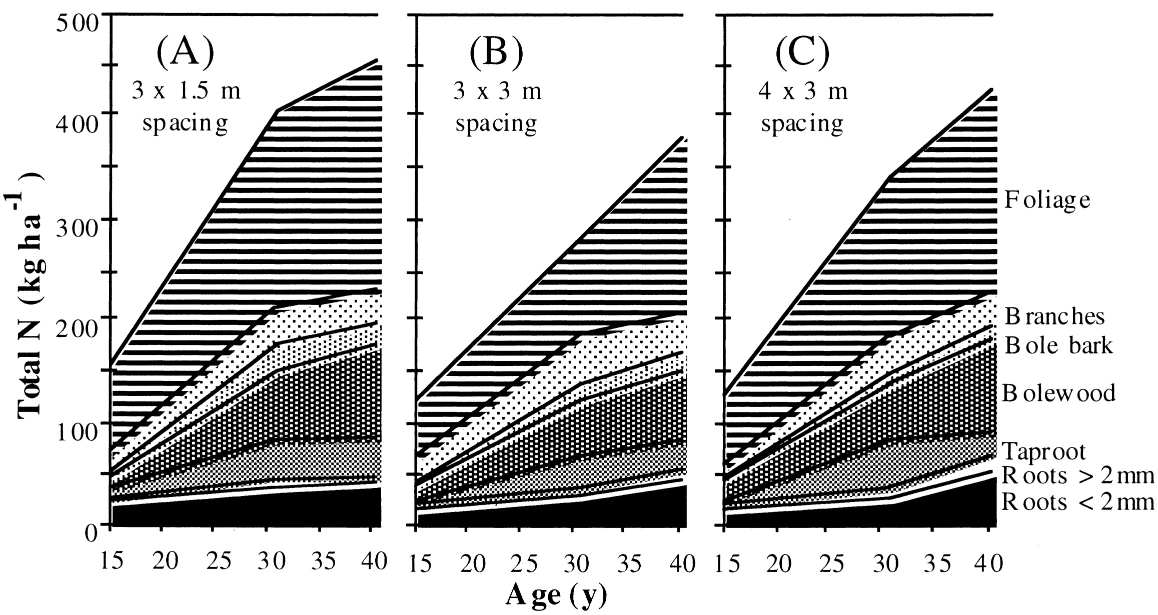

Fig. 2. Average *per hectare* total P pools of tree parts vs. age for *E. urophylla* at (A) 3 m × 1.5 m, (B) 3 m × 3 m and (C) 4 m × 3 m spacing levels.

increase in total P per hectare is not as great as the increase in raw biomass. For instance, Table 5 shows the percent increase in nutrient efficiency (average of all 27 plots) for individual tree parts from age 15 to 41 months. The increase in efficiency is 171% for the bole (wood + bark) and 103% for the whole tree. All tree parts show significant increases in biomass produced per P utilized.

Differences in P with spacing level and age are much greater than for N. For instance, in *E. urophylla* (*E. camaldulensis* and *E. pellita* are similar), total P is much almost twice as high at 15 months for most tree parts in the 3×1.5 compared to the 4×3 spacing level (10.3 vs. 5.4 kg ha^{-1}), indicating a quicker occupancy of the site and quicker accumulation of biomass and nutrients, but by the end of 41 months there are essentially no differences in total P (22 vs. 21 kg ha^{-1}; Fig. 2). Again, increases in nutrient concentration with increased spacing level, which are higher for P than for N (21% vs. 15%; Table 3), accounts for much of this 'evening-out' of total amounts of P per hectare over time compared to the different total biomass amounts.

4. Conclusions

The results of this experiment show the following:

1. Total accumulation of N and P is generally of the order *E. urophylla* > *E. pellita*, *E. camaldulensis*.
2. The concentrations of N and P are generally of the order foliage > branches, bole bark > lateral roots > taproot, bole wood.
3. Total N and P concentrations per unit biomass decreased with increased age, but total content increased.
4. Total N and P concentrations per unit biomass increased with increased spacing level, but total content decreased.
5. In general, relatively small amounts of total tree N and P will be removed in bole-only harvests.

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