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# Production and Nutrient Cycling in Mixed Plantations of *Eucalyptus* and *Albizia* in Hawaii

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**ABSTRACT.** Experimental plantations of pure *Eucalyptus saligna* (Sm.), pure *Albizia falcataria* (L.) Fosberg (a nitrogen-fixing species), and five proportions of mixtures of these species were examined at age 6 for biomass, production, nutrient cycling in litterfall, and resource-use efficiencies. Biomass was greatest in the 34% *Eucalyptus*/66% *Albizia* treatment, averaging 174 Mg/ha, compared with 148 Mg/ha in the fertilized pure *Eucalyptus* treatment and 132 Mg/ha for the pure *Albizia* treatment. The 34% *Eucalyptus*/66% *Albizia* treatment also showed the greatest aboveground net primary production (52 Mg ha<sup>-1</sup> yr<sup>-1</sup>) and annual increment (39 Mg ha<sup>-1</sup> yr<sup>-1</sup>). The N and P content of aboveground litterfall ranged from 35 and 3.5 kg ha<sup>-1</sup> yr<sup>-1</sup> in pure *Eucalyptus* to 240 and 9.5 kg ha<sup>-1</sup> yr<sup>-1</sup> in pure *Albizia*. Nutrient-use efficiency, defined as Mg of ANPP/kg of nutrient in fine litterfall, was greater for *Eucalyptus* (1.1 for N, 13.4 for P) than for *Albizia* (0.2 for N, 5.7 for P). Light-use efficiency ranged from about 14 kJ/MJ of intercepted light in the pure *Albizia* treatment, to 17 kJ/MJ in the pure *Eucalyptus* treatment, to 18 in the 34% *Eucalyptus*/66% *Albizia* treatment. The patterns of productivity across the mixtures resulted from the combination of (1) greater nutrient use efficiency of *Eucalyptus*, (2) greater nutrient cycling under *Albizia*, and (3) greater light capture and high use efficiency in mixed stands. FOR. SCI. 38(2):393-408.

**ADDITIONAL KEY WORDS.** Litterfall, resource-use efficiency, nitrogen, phosphorus, nitrogen fixation.

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**F**AST GROWING TREE SPECIES are the backbone of forest plantations and agroforestry systems covering millions of hectares throughout the humid tropics. Nitrogen availability commonly limits the productivity of these systems, leading to great interest in the development of systems that include nitrogen-fixing trees (National Academy of Sciences 1979, 1984). The success of silvicultural and agroforestry systems that employ N-fixing trees depends strongly on the continued availability of phosphorus, and upon soil pH (many N-fixing leguminous trees are relatively intolerant of acid soils). Intensive management, including frequent harvesting of high-nutrient-content biomass, can lower the availability of all soil nutrients and lead to soil acidification. Species and nutrient cycles may have strong reciprocal effects (Sanchez et al. 1985) that influence the sustainability of intensive forestry and agroforestry. Species differ in the efficiency of biomass production per unit of nutrient taken up from the soil, and in the decomposability of litter (Vitousek 1982). Efficient species that produce large

quantities of biomass per unit of nutrient typically produce litter of poor quality, with the potential to reduce nutrient availability. Species with lower nutrient use efficiencies may produce higher quality litter that could increase nutrient availability. The importance of these possible effects of different tree species remains largely speculative, owing in large part to the paucity of well-designed experimental plantations.

We examined productivity and nutrient cycling in a set of replicated plantations containing pure *Eucalyptus saligna* (Sm.), pure *Albizia falcataria* (L.) Fosberg [= *Paraserianthes falcataria* (L.) Nielsen], and a range of mixtures of these species (described by DeBell et al. 1989). We addressed three major issues:

1. The productivity of monocultures and mixtures;
2. The influence of *Albizia* on nutrient cycling in litterfall;
3. The efficiency of use of nutrients and light, including implications for productivity and nutrient cycling.

## SITE DESCRIPTION

The site is at 480 m elevation, near Hakalau on the northeast coast of Hawaii (about 20 km north of Hilo, DeBell et al. 1989). Annual temperature averages about 21°C ( $\pm 1^\circ\text{C}$  spans the range for all months). Rainfall averages of 4.6 m/yr, and is well distributed through the year (the driest months receive over 150 mm of precipitation). Slopes are gentle ( $<15\%$ ), with soils belonging to the Akaka series (silty clay loam thixotropic isomesic Typic Hydrandep, or with the new Andisol order, probably Typic Hydrudand; R. Yost, University of Hawaii, Honolulu, personal communication). The site was cropped with sugar cane for more than 50 yr, with the last harvest in October 1980. In 1978, 2000 kg/ha of  $\text{CaCO}_3$  were plowed into the soil to raise soil pH for the last crop of sugarcane. The site was plowed in 1981 and regenerating vegetation sprayed with a herbicide before planting in January 1982. Eight stand treatments were evaluated in this study. Treatment #1 was an operational field plantation of *Eucalyptus*, surrounding the four blocks of the main experiment. Treatments #2–8 were established as a study to compare productivity of various ratios of *Eucalyptus* and *Albizia*, using a randomized complete block design (seven treatments in four blocks). Total density was constant (2500 trees/ha) across treatments, which consisted of varying proportions of *Eucalyptus*: 0, 0.34, 0.50, 0.66, 0.75, 0.89, and 1.0. Each plot was 900 m<sup>2</sup>, except the 0.34 and 0.0 *Eucalyptus* plots which were 450 m<sup>2</sup>. Three-month-old containerized seedlings were planted at 2 × 2 m spacing. All plots were fertilized repeatedly (Table 1), but only Treatment #2 (pure *Eucalyptus*) received N after the first year.

At age 4, the biomass of the heavily fertilized, pure *Eucalyptus* treatment (Treatment #2 in Table 1) averaged about 94 Mg/ha, compared with 110 Mg/ha for the pure *Albizia* treatment (Treatment #8; DeBell et al. 1989). At age 8, light extinction by the canopies in the stands that contained *Albizia* ( $>85\%$ ) was much greater than in the pure *Eucalyptus* treatment (66%) (Binkley 1992). In the mixed stands, most of the canopy of *Eucalyptus* was taller than most of the canopy of *Albizia*. Concentrations of both N and P (DeBell et al. 1989) in *Eucalyptus* leaves increased with increasing influence of *Albizia* at 42 months (pure *Eucalyptus*,

TABLE 1.  
Experimental treatments.

Treatment	Species proportion		Fertilization regime (kg/ha)			
	<i>Eucalyptus</i>	<i>Albizia</i>	Month	N	P	K
1	1.0	0	0, 6	40	18	33
2	1.0	0	0, 4, 8, 12, 24, 36 55	40	18	33
3	0.89	0.11	0, 4, 8	40	18	33
4	0.75	0.25	12, 24, 36	18	33	
5	0.66	0.34				
6	0.50	0.50				
7	0.34	0.66				
8	0.0	1.0				

1.8% N, 0.17% P; *Eucalyptus* with *Albizia* 2.1% N, 0.22% P), while foliar manganese declined sharply (to a low of 150 µg/g in *Eucalyptus* with *Albizia*).

## METHODS

### PRODUCTIVITY

Aboveground tree biomass was calculated with regression equations, applied to trees in a central measurement subplot in each plot, at age 5 years and age 6 years (following procedures of DeBell et al. 1989). The equations were developed specifically for these plantations:

$$\textit{Eucalyptus} \text{ biomass (kg)} = 0.01966 (\text{diameter, cm})^{1.9144} (\text{height, m})^{0.9976}$$

(Whitesell et al. 1988)

$$\textit{Albizia} \text{ biomass (kg)} = 0.03621 (\text{diameter, cm})^{2.3146} (\text{height, m})^{0.3600}$$

(Schubert et al. 1988)

Aboveground biomass increment was calculated as the difference between biomass at age 6 and 5; no mortality occurred during this period. Aboveground net primary productivity (ANPP) was calculated as the sum of increment and annual litterfall (described below). The relative yield (Harper 1977) for each treatment was calculated as the ratio of *Eucalyptus* (or *Albizia*) biomass (or increment) of each treatment relative to that found in the pure *Eucalyptus* (or *Albizia*) treatment:

$$\frac{\textit{Eucalyptus}_{\text{mix}}}{\textit{Eucalyptus}_{\text{pure}}}$$

or

$$\frac{\textit{Albizia}_{\text{mix}}}{\textit{Albizia}_{\text{pure}}}$$

The relative yield total for each mixture was the sum of the relative yields for each species. Relative yield totals less than 1 indicate interference between species, whereas totals greater than 1 indicate some divergence in resource use patterns (Harper 1977). In our case, the extra fertilization received by the pure *Eucalyptus* (Treatment #2) may give a relative yield total of less than 1 without indicating interference between species.

#### NUTRIENT CYCLING IN LITTERFALL

Fine litter (primarily leaves, but including fruits, flowers, bark, petioles, and twigs <10 mm in diameter) was collected in six conical (0.25 m<sup>2</sup> surface area) traps per plot of polyethylene mesh suspended 1 m above the ground (Hughes et al. 1987). The traps were placed systematically within each plot in March 1988; the proportion of *Eucalyptus* and *Albizia* trees neighboring the traps corresponded to the proportions of the species in the plot. Litter was collected monthly from April 1988 through March 1989, with collections from the 6 traps/plot composited into single samples for each plot. Woody litter (>10 mm diameter) was collected monthly from two 1 m<sup>2</sup> patches of the soil surface in each plot. Litter was oven-dried at 70°C for 3 to 4 days, then shipped to Colorado State University for analysis. Litter was sorted by species and weighed.

Given the warm, moist environment of the study site, we tested for changes in N concentration of *Eucalyptus* litter sitting in the traps for 4 weeks before collection. Litter samples averaging 540 mg N/g (standard deviation 90) were placed in fine mesh bags within the littertraps; 1 month later, the concentrations averaged 730 mg N/g (standard deviation 180). We therefore expect that decomposition processes may have altered the concentrations of elements in litter before collection (via leaching, respiration weight loss, and perhaps some transfer from *Albizia* litter to *Eucalyptus* litter); given the average residence time of litter in the traps of 1/2 month, we expect the concentration changes to have been at most 15 to 20%.

Nutrient concentrations for fine litterfall were determined for bulk samples from six collection periods (October to March), and these concentrations were multiplied by the annual litter weights to estimate nutrient content of litterfall. Nutrient concentrations for woody materials were determined from subsamples collected in September. Kjeldahl digestions (after Nelson and Sommers 1980) used concentrated sulfuric acid, potassium sulfate, and copper sulfate; digestion was accelerated by additions of hydrogen peroxide after 1 hr and 2 hr of digestion. Digestion was continued for 6 hr after clearing to ensure full recovery of elements from woody materials. Concentrations of N and P in digests were determined on a Lachat Continuous Flow Analyzer, and cations were analyzed by inductively coupled plasma spectroscopy. Recovery from standard pine needles was within 5% for most elements (within 10% for potassium), and recovery of N from standard samples of woody materials (supplied by P. Sollins, Oregon State University) was within 10%.

Four samples of leaf litter from each species (from Treatments #2 and #8) were analyzed for natural abundance of <sup>13</sup>C to check for differences in water use efficiency (Farquhar et al. 1989, Ehleringer and Osmond 1989), and <sup>15</sup>N for differences that might relate to source of nitrogen (Binkley et al. 1985, Shearer and Kohl 1989). Analyses were provided by the Boston University Stable Isotope

Laboratory. Values are reported as parts-per-thousand excess of  $^{13}\text{C}$  ( $\delta^{13}\text{C}$ ) or  $^{15}\text{N}$  ( $\delta^{15}\text{N}$ ) relative to standards (PDB for C, air for N).

Four samples of leaf litter were also analyzed (by J. Pastor, University of Minnesota, Duluth) for the pure *Eucalyptus* stand (Treatment #2), the pure *Albizia* stand (Treatment #8), and for each species in the 50%/50% stand (Treatment #6) for (Ryan et al. 1990): carbon, ash, nonpolar extractives (dichloromethane extract, TAPPI 1976), boiling water-soluble fraction (TAPPI 1975), acid soluble residue (holocellulose), acid insoluble residue (lignin), and tannin.

We used the GEM (General Ecosystem Model) decomposition model (Rastetter et al. 1991, Ryan et al. in prep.) to assess the influence of litter quality on litter decomposition and N mineralization. GEM simulates the decomposition of a litter cohort under constraints of temperature and moisture, based on initial concentrations of: nitrogen, extractives (total polar and nonpolar), cellulose, and lignin expressed as a percent of ash-free dry weight. Intensive work on *Eucalyptus* decomposition (O'Connell 1988) supports the importance of ratios of lignin:nutrients in controlling decomposition, but no similar data are available for *Albizia*. To estimate the time course of N release from decomposing litter, we used values of litter quality as initial conditions, temperature of 21°C, assumed optimum soil moisture, and ran the model for 50 months. The calibration data used in the development of GEM (and the relationships between decomposition and moisture and temperature) did not include any tropical forests, and we suspect that N dynamics in decomposing litter may be somewhat faster in tropical situations than the model suggests. However, the relative patterns between species (which depend on litter quality rather than site conditions) should be realistic.

#### RESOURCE USE EFFICIENCY

The efficiency of using N and P could be calculated as the Mg of aboveground net primary production per kg of nutrient taken up. We have no direct estimates of nutrient uptake, so we used the nutrient content of fine litterfall as a surrogate (after Vitousek 1982), and calculated nutrient use efficiency as Mg of ANPP/kg of nutrient in fine litterfall.

Light use efficiency was calculated as the energy content of ANPP (taken at 17.7 kJ/g ANPP from Whittaker 1975) divided by the cumulative annual light (photosynthetically active radiation) interception. The proportion of incoming light intercepted by the canopy was taken from Binkley (1992; determined with a Decagon Ceptometer), and multiplication by an estimated annual solar insolation of 5500 MJ/m<sup>2</sup> (J. Juvik, University of Hawaii-Hilo, personal communication) provided an estimate of cumulative annual light interception. These values at age 8 may not match actual light interception at age 6, when the two-storied structure of the stands was less pronounced, but we feel they provide realistic relative comparisons.

Statistical differences were assessed using analysis of variance, with seven (for productivity and biomass data) or eight (for litterfall) treatments replicated in four blocks. Significant effects were examined with Tukey's Honestly Significant Difference test, with a probability of a Type I error of 0.1 (SYSTAT version 5.0, 1990). The variances of the litter quality data were not equal across treatments, so means were compared using the Kruskal-Wallis analysis of variance and Mann-Whitney U test.

## RESULTS AND DISCUSSION

### PRODUCTIVITY

Stand biomass at age 6 (Figure 1) appeared greatest in Treatment #7 (34% *Eucalyptus*/66% *Albizia*), but the differences among treatment means were not significant ( $P = 0.23$ ) (data for Treatment #1, the pure *Eucalyptus* field plantation, are not available). Annual biomass increment followed a similar trend, with significant differences among means. The 34% *Eucalyptus*/66% *Albizia* treatment (#7) showed the maximum average biomass (about 174 Mg/ha), increment (about 39 Mg ha<sup>-1</sup> yr<sup>-1</sup>), and aboveground net primary production (52 Mg ha<sup>-1</sup> yr<sup>-1</sup>). The poorest treatment (#3) was the 89% *Eucalyptus*/11% *Albizia*; the presence of a small proportion of *Albizia* could not compensate for the lower fertilization regime. These trends in biomass show substantial shifts in the ranking of treatment since age 4 yr, when DeBell et al. (1989) found greatest biomass in the pure *Albizia* treatment.

The relative yield totals (Figure 2) were less than 1.0 for Treatments #3 (89% *Eucalyptus*) and #4 (75% *Eucalyptus*), and greater than 1.0 for Treatments #6 (0.50 *Eucalyptus*) and #7 (34% *Eucalyptus*). Relative yield totals less than 1 suggest that inclusion of low proportions of *Albizia* did not improve the N nutrition of *Eucalyptus* on par with the repeated N fertilization of Treatment #2, or that inclusion of low proportions of *Albizia* impeded *Eucalyptus* growth (per ha) and high proportions of *Eucalyptus* impaired *Albizia* growth. When the proportion of *Albizia* comprised one-third or more of the stand, competition between species appeared less critical; the species appeared to make different demands on resources (see Chapter 8 of Harper 1977 for a general discussion of relative yield totals). The increment at age 6 in Treatment #7 was especially impressive, with a relative yield total of almost 1.6.

### NUTRIENT CYCLING IN LITTERFALL

The seasonal pattern of fine litterfall showed peaks in August and December, with the August peak being more pronounced for *Eucalyptus* and the December peak more pronounced for *Albizia* (Figure 3). Seasonal patterns appeared similar across treatments, depending on species but not on species mixtures. The annual total litterfall biomass increased with increasing proportion of *Albizia*, though the only significant differences were between the two pure *Eucalyptus* treatments (#1 and #2) and the pure *Albizia* treatment (#8). The two pure *Eucalyptus* treatments were essentially identical in litterfall biomass and nutrient content, indicating little current effect of the additional fertilization in Treatment #2. Litterfall biomass ranged from about 7–9 Mg ha<sup>-1</sup> yr<sup>-1</sup> in the pure *Eucalyptus* treatment, to 12–13 Mg ha<sup>-1</sup> yr<sup>-1</sup> in the mixed species treatments, to about 18 Mg ha<sup>-1</sup> yr<sup>-1</sup> in the pure *Albizia* treatment (Figure 3). The pure *Albizia* plots were small enough that *Eucalyptus* litter from adjacent plots comprised about 5% of the litter collected in the pure *Albizia* plots. Differences in the N content of litter followed the same pattern (Figure 4), but were more pronounced: 30–40 kg ha<sup>-1</sup> yr<sup>-1</sup> in pure *Eucalyptus*, 110–140 kg ha<sup>-1</sup> yr<sup>-1</sup> in the mixtures, and about 240 kg ha<sup>-1</sup> yr<sup>-1</sup> in the pure *Albizia*. This pattern was repeated for phosphorus, potassium, and magnesium, but calcium showed no clear pattern across treat-

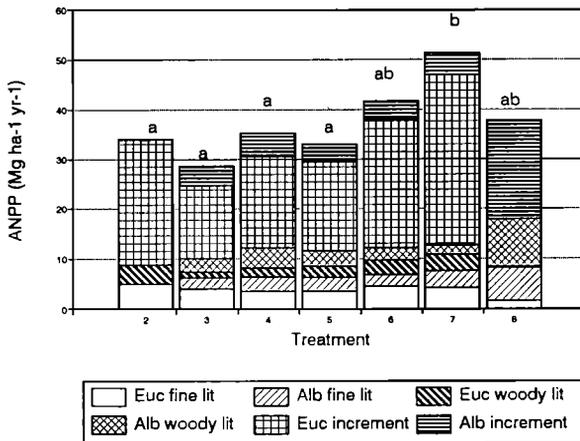
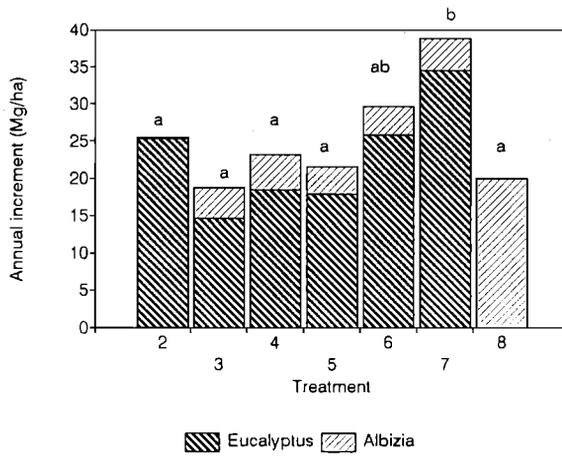
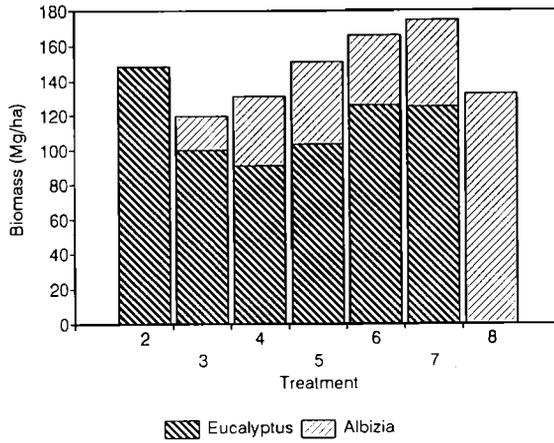


FIGURE 1. Stand biomass at age 6 (top), annual increment (middle), and aboveground net primary production (bottom). Common letters among columns indicate means do not differ at  $P = 0.1$ .

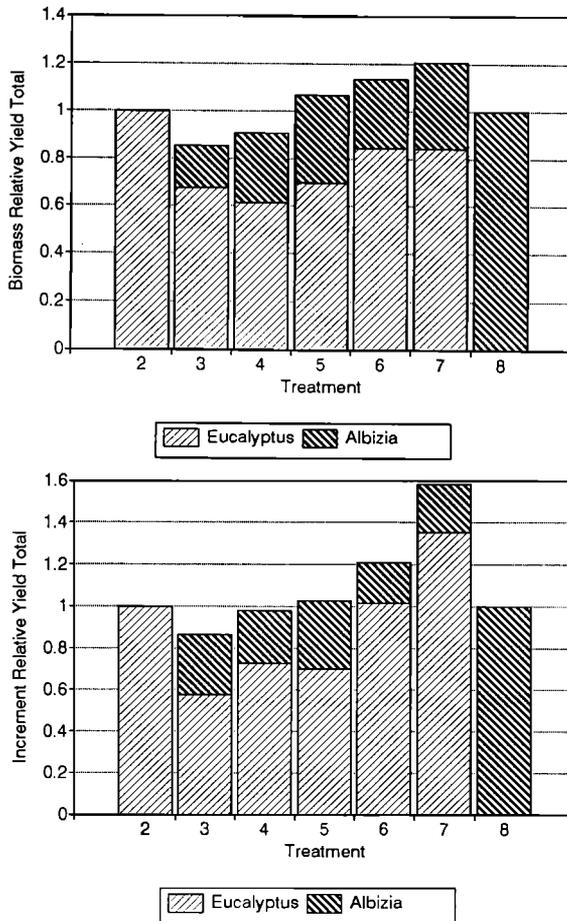


FIGURE 2. Relative yields of each species in each treatment, and relative yield totals for each treatment.

ments. Woody materials contributed a substantial portion (up to half) of litterfall biomass, N and P in all treatments.

The ratio of stable isotopes of C and N in leaf litter from the pure stands showed no significant differences between species: *Eucalyptus*  $\sigma^{13}\text{C}$ -29.9 (standard deviation 0.4),  $\sigma^{15}\text{N}$  - 1.5 (0.7); *Albizia*  $\sigma^{13}\text{C}$  - 29.9 (0.3),  $\sigma^{15}\text{N}$  - 1.0 (0.5). The  $\sigma^{13}\text{C}$  indicates both species have low water-use efficiency (Ehleringer and Osmond 1989), which is not surprising in this high rainfall environment. The slightly negative  $\sigma^{15}\text{N}$  for both species indicates that available nitrogen in the soil differs little in isotope ratio from the atmosphere, providing no opportunity for tracing N fixed by *Albizia* through the ecosystem.

The quality of litter differed substantially between the species (Table 2). *Eucalyptus* leaf litter was lower in N, cellulose, and lignin than *Albizia* leaf litter, whereas *Albizia* leaf litter was lower in nonpolar extractives, polar extractives, and tannin. In the field, very few *Albizia* leaves could be found on the soil surface despite the high rate of litterfall. We did not measure the biomass of *Eucalyptus* leaves on the soil surface, but it appeared to be only a few months worth of

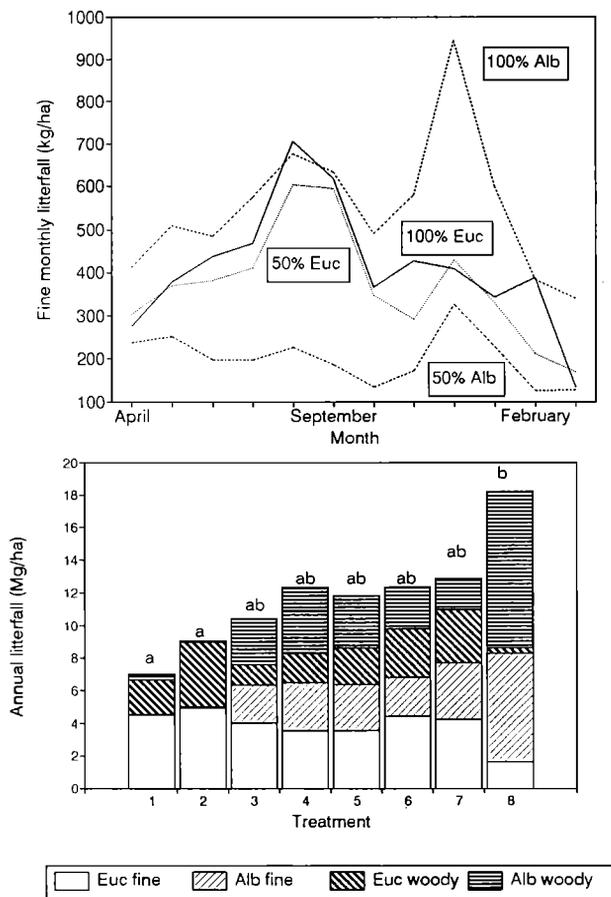


FIGURE 3. Seasonal pattern of litterfall (upper) for *Eucalyptus* and *Albizia* in the pure treatments and in the 50%/50% mixture, and annual total litterfall (lower). Common letters among columns indicate means do not differ at  $P = 0.1$ .

litterfall. The rapid disappearance of materials in the forest floor might indicate very rapid decomposition, or physical mixing of the materials into the mineral soil by earthworms. Earthworm numbers were 5-fold greater in the pure *Albizia* treatment ( $469/m^2$ ) than in the pure *Eucalyptus* treatment ( $92/m^2$ ; Zou 1991).

The GEM simulation showed that nitrogen should be released rapidly from the *Albizia* leaves (Figure 5), while the *Eucalyptus* should accumulate N from the soil for a substantial period before showing any net release. About half of the N in *Albizia* litter may be released in 8 months, but no net release was projected after 50 months for *Eucalyptus*.

The greater rate of N cycling in litterfall in treatments containing *Albizia* was expected; although we have no estimates of N fixation, root nodules were commonly encountered in soil pits, and we expect N fixation rates to have been substantial. If actual N-fixation rates were low, then the increase in N-cycling in *Albizia* would have resulted from some species-specific ability to tap and cycle N from pre-existing pools in the soil. The increased cycling of P in the N-fixing

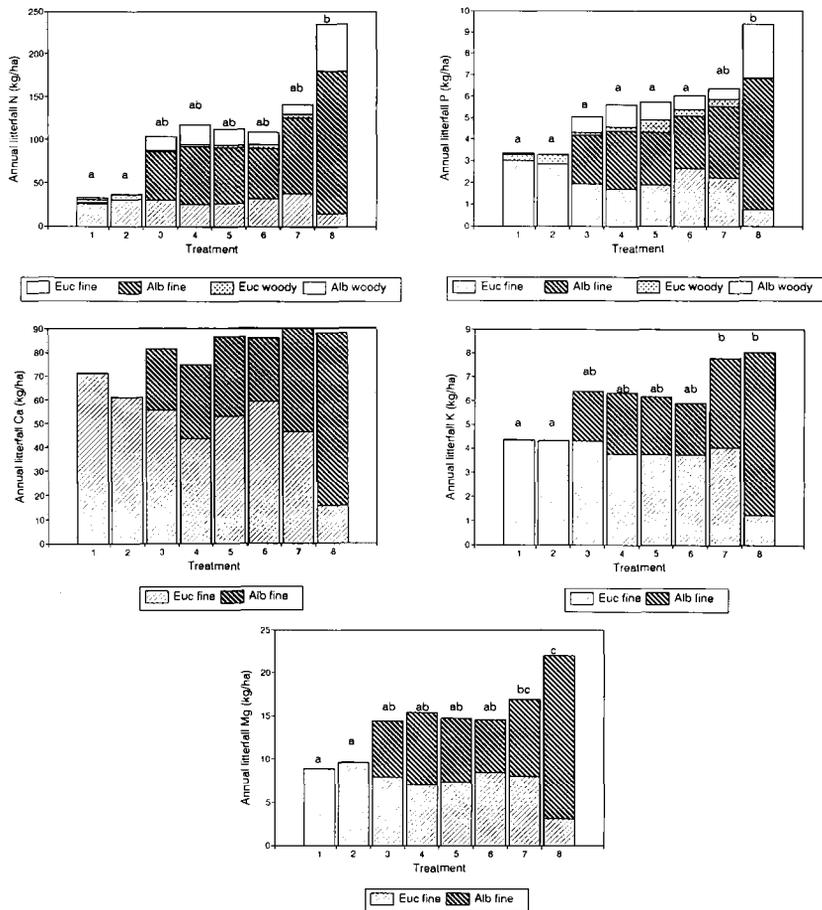


FIGURE 4. Nutrient content of litterfall. Common letters among columns indicate means do not differ at  $P = 0.1$ .

*Albizia* treatments was surprising. Higher P cycling coupled with improved P nutrition of *Eucalyptus* grown with *Albizia* (DeBell et al. 1989) may have widespread implications for the incorporation of N-fixing trees in silvicultural and agroforestry systems. Sustained productivity may depend on high inputs of N from N-fixing species, and high rates of N fixation may depend on continued availability of P. Increased P availability under *Albizia* may lead to both improved P nutrition on P-limited sites, and increased rates of N fixation.

Stands containing N-fixing trees generally show greater cycling of phosphorus in litterfall than stands without N-fixing trees (Binkley 1992). The controls on P availability include simple rooting profiles (Malcolm et al. 1985), as well as more complex geochemical reactions (such as acidification, Gillespie and Pope 1990a,b) and biologic processes involving exocellular enzymes (Ho 1979), organic chelates (O'Connell et al. 1983, Reid et al. 1985, Jurinak et al. 1986, Ae et al. 1990), and mycorrhizae (Mulette et al. 1974, Schoeneberger 1984, Attiwill and Leeper 1987). Each of these mechanisms may have been important in controlling the availability of P to *Eucalyptus* and *Albizia* in our plantations, as well as in other situations around the world. A great deal more research is warranted to identify

TABLE 2.

Litter quality, mean of four samples in mg/g oven-dry weight (standard deviation). All means differed significantly between species (at  $P < 0.01$  or less). Within species, common letters denote means that do not differ at  $P = 0.1$ .

Species	Treatment	C	N	Extractable			Cellulose	Lignin	Polyphenols (mg/g polar ext.)
				Nonpolar	Polar				
<i>Eucalyptus</i>	2	530 (6)a	8.9 (0.3)	156 (10)	213 (20)a	355 (45)	276 (30)	74 (20)a	
<i>Eucalyptus</i>	6	540 (6)b	8.7 (0.1)	172 (24)	176 (27)b	391 (7)	261 (17)	53 (11)b	
<i>Albizia</i>	6	500 (10)	23.5 (0.3)	57 (21)	118 (32)	462 (26)a	364 (53)	13 (2)	
<i>Albizia</i>	8	510 (3)	23.0 (0.1)	56 (9)	91 (25)	432 (7)b	422 (24)	11 (1)	

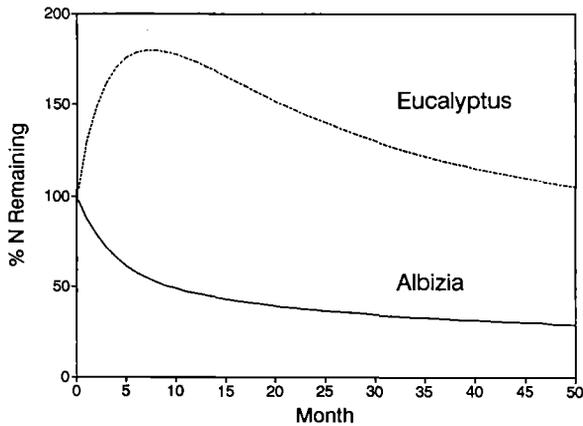


FIGURE 5. GEM simulation of N dynamics in decomposing leaf litter for the pure *Eucalyptus* and pure *Albizia* treatments.

the most important mechanism and to examine their importance across species and regions.

#### RESOURCE-USE EFFICIENCIES

Nutrient-use efficiency was much higher in treatments circulating low quantities of nutrients in aboveground litterfall, indexed as Mg of ANPP per kg of nutrient cycled in fine litterfall (Figure 6). The highest efficiencies were found in the pure *Eucalyptus* treatment, and lowest in the pure *Albizia* treatment. In a literature synthesis, Vitousek (1982) suggested that litterfall biomass may substitute as an index of net primary production, and calculated an index of nutrient use efficiency as the reciprocal of the nutrient concentration of aboveground litterfall. Nutrient use efficiencies declined as the quantity of nutrients cycling in litterfall increased (Vitousek 1982). Our plantations followed this expected pattern, when either ANPP or litterfall biomass was used as the measure of ecosystem productivity. The correlations between our index of nutrient-use efficiency (using ANPP directly) and the one used by Vitousek (using litterfall biomass as a surrogate for ANPP) were quite strong ( $r^2 = 0.87$  for N, and 0.72 for P). Vitousek noted that the pattern of declining nutrient-use efficiency with increasing nutrient cycling rates could result from autocorrelation (the nutrient content of litterfall is included on both axes), but showed that the pattern across sites in his literature summary deviated substantially from the trend expected from simple autocorrelation. In our study within a single site, the trend of declining nutrient use efficiency primarily resulted from simple autocorrelation between the axes.

The rates of nitrogen cycling in litterfall in the pure *Eucalyptus* treatments (25 to 45 kg ha<sup>-1</sup> yr<sup>-1</sup>) are within the ranges reported for other *Eucalyptus* stands by Adams and Attiwill (1986), Attiwill and Leeper (1987), and Kieth (1991), and the range for montane tropical forests (Vitousek 1984). No rates of litterfall nitrogen are available for other *Albizia* stands, but our rates for stands with *Albizia* (100–240 kg ha<sup>-1</sup> yr<sup>-1</sup>) are in the upper range for tropical lowland forests (Vitousek 1984).

Light interception in the 34% *Eucalyptus*/66% *Albizia* was 39% greater than in the pure *Eucalyptus* treatment (Table 3), and light use efficiency was marginally

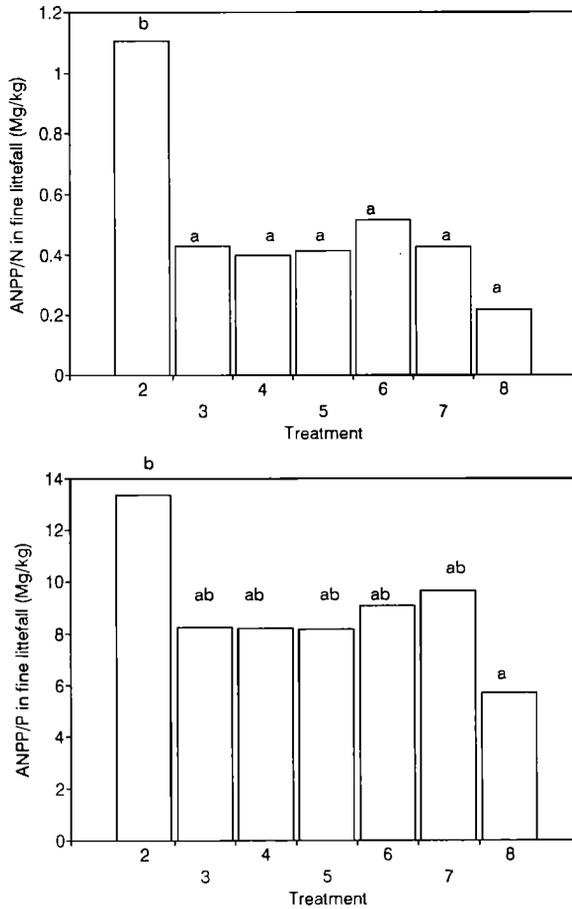


FIGURE 6. Nutrient use efficiencies. Common letters among columns indicate means do not differ at  $P = 0.1$ .

greater (by 8%); the combination of greater light interception and use efficiency combined to increase ANPP by 50%. Light capture in the pure *Albizia* treatment was 33% greater than in the pure *Eucalyptus* treatment, but the light use efficiency was 17% lower; the combination of these offsetting effects was 10% greater ANPP in the pure *Albizia* treatment.

TABLE 3.

Light-use efficiencies.

Treatment	Mixture <i>Eucalyptus/Albizia</i>	ANPP $\text{MJ m}^{-2} \text{yr}^{-1}$	Light intercepted $\text{MJ m}^{-2} \text{yr}^{-1}$	Light-use efficiency $\text{kJ/MJ}$
2	100/0	61	3630	16.8
4	75/25	63	4780	13.2
7	34/66	92	5045	18.2
8	0/100	68	4840	14.0

## CONCLUSIONS

These plantations demonstrated dramatic differences among species and combinations of species on stand productivity, nutrient cycling, and resource-use efficiencies. *Eucalyptus* used nutrients more efficiently than *Albizia*, but *Albizia* showed greater cycling of nutrients, and species mixtures demonstrated greater light interception. Greater nutrient cycling rates in treatments with *Albizia* coupled with greater nutrient-use efficiency by *Eucalyptus* allows opportunities for greater stand productivity in mixed stands than in pure stands of either species. Major questions remain about the biogeochemical mechanisms underlying these effects, the sustainability of the effects, and how the patterns found in this plantation would extrapolate to other sites. Given the dramatic evidence of major effects, we hope that major research efforts can be developed to address these questions about mixed-species plantations.

## LITERATURE CITED

- AE, N., J. ARIHARA, K. OKADA, T. YOSHIHARA, and C. JOHANSEN. 1990. Phosphorus uptake by pigeon pea and its role in cropping systems of the Indian subcontinent. *Science* 248:477-480.
- ADAMS, M.A., and P.M. ATTIWILL. 1986. Nutrient cycling and nitrogen mineralization in eucalypt forests of south-eastern Australia. *Plant Soil* 92:319-339.
- ATTIWILL, P.M., and G.W. LEEPER. 1987. *Forest soils and nutrient cycles*. Melbourne University Press, Melbourne.
- BINKLEY, D. 1992. Mixtures of N<sub>2</sub>-fixing and non-N<sub>2</sub>-fixing tree species. P. 99-123 in *the ecology of mixed species stands*, Cannell, M., and D. Malcolm (eds.). Blackwell Scientific, Oxford.
- BINKLEY, D., P. SOLLINS, and W. MCGILL. 1985. Natural abundance of nitrogen-15 as a tool for tracing alder-fixed nitrogen. *Soil Sci. Soc. Am. J.* 49:444-447.
- DEBELL, D.S., C.D. WHITESELL, and T.H. SCHUBERT. 1989. Using N<sub>2</sub>-fixing *Albizia* to increase growth of *Eucalyptus* plantations in Hawaii. *For. Sci.* 35:64-75.
- EHLERINGER, J.R., and C.B. OSMOND. 1989. Stable isotopes. P. 281-300 in *Plant physiological ecology: Field methods and instrumentation*, Pearcy, R., J. Ehleringer, H. Mooney, and P. Rundel (eds.). Chapman and Hall, New York.
- FARQUHAR, G., K. HUBICK, A. CONDON, and R. RICHARDS. 1989. Carbon isotope fractionation and plant water-use efficiency. P. 21-40 in *Stable isotopes in ecological research*, Rundel, P., J. Ehleringer, and K. Nagy (eds.). Springer-Verlag, New York.
- GILLESPIE, A.R., and P.E. POPE. 1990a. Rhizosphere acidification increases phosphorus recovery of black locust: I. Induced acidification and soil response. *Soil Sci. Soc. Am. J.* 54:533-537.
- GILLESPIE, A.R., and P.E. POPE. 1990b. Rhizosphere acidification increases phosphorus recovery of black locust: II. Model predictions and measured recovery. *Soil Sci. Soc. Am. J.* 54:538-541.
- HARPER, J. 1977. *Population biology of plants*. Academic Press, New York.
- HUGHES, J.W., T.J. FAHEY, and B. BROWNE. 1987. A better seed and litter trap. *Can. J. For. Res.* 17:1623-1624.
- JURINAK, J.J., L.M. DUDLEY, M.F. ALLEN, and W.G. KNIGHT. 1986. The role of calcium oxalate in the availability of phosphorus in soils of semiarid regions: A thermodynamic study. *Soil Sci.* 142:255-261.
- HO, I. 1979. Acid phosphatase activity in forest soil. *For. Sci.* 25:567-568.
- KEITH, H. 1991. Effects of fire and fertilization on nitrogen cycling and tree growth in a subalpine eucalypt forest. Ph.D. thesis, Australian National University, Canberra.
- MALCOLM, D., J. HOOKER, and C. WHEELER. 1985. *Frankia* symbiosis as a source of nitrogen in forestry: A case study of symbiotic nitrogen-fixation in a mixed *Alnus-Picea* plantation in Scotland. *Proc. Royal Soc. Edinburgh* 85B:263-282.

- MULETTE, K., N. HANNON, and A. ELLIOTT. 1974. Insoluble phosphorus usage by *Eucalyptus*. *Plant Soil* 41:199-205.
- NATIONAL ACADEMY OF SCIENCES. 1979. Tropical legumes: Resources for the future. National Academy Press, Washington, DC.
- NATIONAL ACADEMY OF SCIENCES. 1984. Leucaena: Promising forage and tree crop for the tropics. National Academy Press, Washington, DC.
- NELSON, D., and L. SOMMERS. 1980. Total nitrogen of soil and plant tissue. *J. Assoc. Anal. Chem.* 63:770-778.
- O'CONNELL, A.M. 1988. Nutrient dynamics in decomposing litter in Karri (*Eucalyptus diversicolor* F. Muell.) forests of south-western Australia. *J. Ecol.* 76:1186-1203.
- O'CONNELL, A.M., N. MALAJCZUK, and V. GAILITIS. 1983. Occurrence of calcium oxalate in Karri (*Eucalyptus diversicolor* F. Muell.) forest ecosystems of southwestern Australia. *Oecologia* 56:239-244.
- RASTETTER, E., ET AL. 1991. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO<sub>2</sub>, climate, and N deposition. *Tree Physiol.* 9:101-126.
- REID, R.K., C.P.P. REID, and P.J. SZANISZLO. 1985. Effects of synthetic and microbially produced chelates on the diffusion of iron and phosphorus to a simulated root in soil. *Biol. Fert. Soils* 1:45-52.
- RYAN, M.G., J.M. MELILLO, and A. RICCA. 1990. A comparison of methods for determining proximate carbon fractions of forest litter. *Can. J. For. Res.* 20:166-171.
- RYAN, M.G., ET AL. In preparation. A general model of decomposition and soil and C and N dynamics for estimating the effects of climate change on the biogeochemistry of temperate terrestrial ecosystems.
- SANCHEZ, P.A., C.A. PALM, C.B. DAVEY, L.T. SZOTT, and C.E. RUSSELL. 1985. Tree crops as soil improvers in the humid tropics? P. 327-358 in *Attributes of trees as crop plants*, Cannell, M., and J.E. Jackson (eds.). Institute of Terrestrial Ecology, Huntington, England.
- SCHOENEBERGER, M.M. 1984. Endophytes of *Eucalyptus*. P. 444 in *Proc. 6th North Am. Conf. on Mycorrhizae*, Molina, R. (ed.). Forest Research Laboratory, Oregon State University, Corvallis.
- SCHUBERT, T.H., R.F. STRAND, T.G. COLE, and K.E. McDUFFIE. 1988. Equations for predicting biomass of six introduced tree species, Island of Hawaii. *USDA For. Serv. Res. Note PSW-401*.
- SHEARER, G., and D. KOHL. 1989. Estimates of N<sub>2</sub> fixation in ecosystems: The need for and basis of the <sup>15</sup>N natural abundance method. P. 342-374 in *Stable isotopes in ecological research*, Rundel, P., J. Ehleringer, and K. Nagy (eds.). Springer-Verlag, New York.
- SOLLINS, P., K. CROMACK, JR., C.Y. LI, and R. FOGEL. 1981. Role of low-molecular-weight organic acids in the inorganic nutrition of fungi and higher plants. P. 607-619 in *The fungal community: Its organization and role in the ecosystem*, Wicklow, D.T., and G.C. Carroll (eds.). Marcel Dekker, New York.
- SYSTAT. 1990. SYSTAT Version 5.0. SYSTAT Inc., Evanston, IL.
- TAPPI. 1975. Water solubles in wood and pulp. *Technical Assoc. of the Pulp and Paper Industry T207*.
- TAPPI. 1976. Alcohol-benzene and dichloromethane solubles in wood and pulp. *Technical Assoc. of the Pulp and Paper Industry T204*.
- VITOUSEK, P.M. 1982. Nutrient cycling and nutrient efficiency. *Am. Natur.* 119:553-572.
- VITOUSEK, P.M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285-298.
- WHITESSELL, C.D., S.C. MIYASAKA, R.F. STRAND, T.H. SCHUBERT, and K.E. McDUFFIE. 1988. Equations for predicting biomass in 2- to 6-year-old *Eucalyptus saligna* in Hawaii. *USDA For. Serv. Res. Note PSW-402*.
- WHITTAKER, R.H. 1975. *Communities and ecosystems*. Macmillan, New York.
- ZOU, X. 1992. Phosphorus transformations in soils: A new method and tree species effects. Ph.D. diss., Colorado State University, Fort Collins.

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Binkley is professor and Dunkin was a graduate research assistant (now at the Department of Soil Science at the University of California, Berkeley, CA) in the Department of Forest Sciences at Colorado State University, Ft. Collins, CO 80523. DeBell is a silviculturist with the USDA Forest Service Pacific Northwest Research Station, Olympia, WA; and Ryan is a Forest Ecologist with the USDA Forest Service Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO. The plantations were established and biomass measured with funds from the Department of Energy, through Oak Ridge National Laboratory, subcontract #19X-09061C; with interagency agreement #DE-AI05-860421661; the nutrient cycling work was funded by McIntire-Stennis appropriations to Colorado State University. For outstanding help in the office, lab, and field, we thank C.D. Whitesell, T.H. Schubert, R.F. Strand, T.G. Cole, U. Reisenkonig, D. Valentine, and technical support personnel of the USDA Forest Service Pacific Southwest Research Station and the BioEnergy Development Corporation. We thank J. Pastor for the litter carbon chemistry, and M. Schoeneberger, B. Caldwell, and two anonymous reviewers for help with the manuscript.