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Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico

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Abstract

Tree growth, biomass productivity, litterfall mass and nutrient content, changes in soil chemical properties and understory forest succession were evaluated over a 8.5-year period in single- and mixed-species (50 : 50) plantations of two N_2-fixing species, *Casuarina equisetifolia* and *Leucaena leucocephala*, and a non-fixing species, *Eucalyptus robusta*. At the optimal harvest age for maximum biomass production (4 years), total aboveground biomass ranged from 63 Mg ha^{-1} in the *Eucalyptus* monoculture to 124 Mg ha^{-1} in the *Casuarina/Leucaena* mixture, and was generally greater in the mixed-species than in single-species treatments due to increased productivity of the N-fixing species in the mixed stands. Total litterfall varied from 5.3 to 10.0 Mg ha^{-1} $year^{-1}$ among treatments, or between 5.9% and 13.2% of net primary production. Litterfall production and rates of nutrient return for N, P, K, Ca and Mg were generally highest for *Leucaena*, intermediate for *Casuarina* and lowest for *Eucalyptus*. These rates were usually higher in the mixed-species than in monospecific stands due to differences in biomass productivity, but varied considerably depending on their species composition. Total system carbon and nutrient pools (in biomass plus soils to 40-cm depth) for N, P, K, Ca, Mg, Mn at four years were consistently greater in the plantation treatments than in the unplanted control plots. Relative to the single-species plantations, these system pools were generally larger in the mixed-species plantations for C (−10% to +10%), N (+17% to +50%), P (−1% to +63%), K (−19% to +46%), Ca (−10% to +48%), Mg (+5% to +57%) and Mn (+19% to +86%). Whole-tree harvests at four years would result in substantial system carbon and nutrient losses, although these estimated losses would not exceed the estimated gains realized during the four-year period of tree growth at this site. At 7.5 years, soil organic matter and effective cation exchange capacity were reduced in all plantation treatments relative to the control. Changes in soil nutrient content from 0 to 7.5 years were highly variable and not significantly different among treatments, although stands containing *Leucaena* generally showed higher rates of nitrogen and phosphorus accretion in soils than those with *Eucalyptus* and/or *Casuarina*. Natural regeneration of secondary forest tree and shrub species increased over time in all plantation treatments. A total of 24 native or naturalized forest species were recorded in the plantations at 8.5 years. Woody species abundance at this age was significantly greater beneath *Casuarina* than either *Eucalyptus* or the *Eucalyptus/Leucaena* mixed stands. Species richness and diversity, however, were greatest beneath stands containing *Eucalyptus* and/or *Leucaena* than in stands with *Casuarina*.

Keywords: Biomass productivity; *Casuarina*; *Eucalyptus*; Floristic diversity; *Leucaena*; Litterfall; Nitrogen-fixing trees; Plantations; Soils; Tropics

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1. Introduction

Plantations of fast growing native and exotic trees are assuming an increasingly significant role in landscape management and the rural economy in many tropical regions (FAO, 1993; National Research Council, 1993). Such plantations provide fuel, small-dimension timber, and non-wood forest products for local communities, and are being used increasingly for rehabilitating deforested watersheds and other degraded landscapes, particularly in densely populated tropical regions (Evans, 1992; Brown and Lugo, 1994; Brown et al., 1997). According to United Nations estimates, tree planting for non-industrial uses (i.e. woodlots for fuel and locally used timber, agroforestry plantings, and plantations established primarily for rehabilitation of deforested watersheds) increased dramatically between 1981 and 1990. During this period, ≈12 million ha, or 64% of all new plantations in tropical countries, were established for these purposes. In 1990, the total non-industrial plantation area in the tropics was estimated at 28.2 million ha, of which 82% is found in the Asia and Pacific region, 12% in Latin America and the Caribbean, and 6% in Africa (FAO, 1993).

The promotion of short-rotation plantations, as a solution to the chronic wood shortages faced by hundreds of millions of people in tropical regions (FAO, 1981), has raised concerns about their sustainability. Of particular concern is the risk that frequent harvest-related nutrient losses could result in soil fertility and biomass productivity declines over successive rotations, particularly on inherently infertile or otherwise degraded soils where such plantations are often established (Jorgensen et al., 1975; Kimmins, 1977; Wise and Pitman, 1981; Jorgensen and Wells, 1986; Gonçalves et al., 1997). Earlier research has clearly shown that tree species differ widely in their nutrient uptake, storage and recycling patterns (Lugo, 1992a; Cuevas and Lugo, 1998). As a result, harvest-related nutrient ‘costs’ per unit of wood or total biomass production also greatly vary (da Silva et al., 1983; Wang et al., 1991; Toky and Singh, 1995; Fölster and Khanna, 1997). While these system nutrient exports can be reduced by harvesting and removing only stemwood and large-diameter branchwood, rather than total aboveground biomass (Kimmins, 1977; Johnson, 1983; Parrotta, 1989; Wang et al., 1991; Montagnini and Sancho, 1994; Fölster and Khanna, 1997), this may not be a practical option in many, perhaps most, rural tropical areas where people use twigs, foliage and even leaf litter for fuel, livestock fodder, and mulch.

Nitrogen-fixing trees, mainly leguminous species, have been widely extolled for their soil-improving characteristics related to their production of nitrogen-rich, often rapidly decomposed, leaf litter (National Academy of Sciences, 1979; Werner and Muller, 1990; MacDicken, 1994). These species are commonly used in agroforestry systems worldwide to great benefit, and have been recommended for mixed-species plantings with other, perhaps more highly valued tree species to help offset potential soil nitrogen deficiencies and increase overall biomass productivity. Although there have been some documented cases of increased productivity in mixed-species plantations in both, temperate and tropical regions, the collective results of such studies have been inconclusive and show that accurate species/site matching and choice of complementary species strongly influence mixed-species plantation productivity (FAO, 1992).

Another set of concerns raised by critics of short-rotation tropical plantations and monospecific rehabilitation plantation programs revolve around the (common) use of exotic species and their effects on soil fertility and biodiversity. It is often alleged that exotic species, particularly *Eucalyptus* species, more rapidly deplete soil nutrients and water, and that they inhibit the development of native flora in their understories. Although the available evidence rarely, if ever, supports these allegations (see, for example, Poore and Fries, 1985; George et al., 1993; Lugo, 1992b, 1997; Lugo et al., 1993; Silva Junior et al., 1995; Bone et al., 1997; Fang and Peng, 1997; Geldenhuys, 1997; Harrington and Ewel, 1997; Loumeto and Huttel, 1997; Parrotta et al., 1997; Parrotta and Knowles, 1999), these concerns persist, particularly among many restoration ecologists and conservation biologists.

In order for these managed forest systems to continue to provide social, economic and environmental benefits over successive harvest rotations, a better understanding of tree species' impacts on various aspects of soil fertility, including nutrient cycling processes, is therefore essential. In the case of plantations established primarily for rehabilitation of severely degraded sites, watershed stabilization, and/ or native forest restoration, additional knowledge of how planted trees can facilitate, or inhibit, natural successional processes that lead to the development of structurally diverse and functionally stable forest ecosystems is also needed.

The present study was undertaken to assess biomass productivity, biomass nutrient storage and recycling, soil-nutrient storage patterns, and plantation effects on understory succession over an 8.5-year period in single- and mixed-species stands established on a degraded coastal site in Puerto Rico. These experimental plantations included three extensively planted tropical tree species: two N_2-fixing species (*Casuarina equisetifolia* and *Leucaena leucocephala*) and *Eucalyptus robusta*. In this paper, study data will be used to test the hypotheses that mixed-species plantations are more productive, have higher rates of nutrient return through litterfall, have a more significant positive effect on soil-fertility parameters, and provide a more favorable environment for understory forest succession over time than single-species plantations.

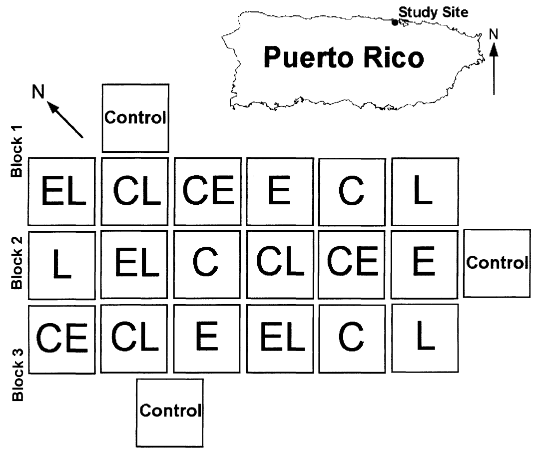

Fig. 1. Study site location and experimental plot layout. Plot treatment codes: C, *Casuarina* monoculture; E, *Eucalyptus* monoculture; L, *Leucaena* monoculture; CE, *Casuarina* + *Eucalyptus*; CL, *Casuarina* + *Leucaena*; EL, *Eucalyptus* + *Leucaena*; and Control, unplanted plots.

2. Materials and methods

2.1. Experimental plantation design

The study area is located at the University of Puerto Rico's Toa Baja experiment station, on the northern (Atlantic) coast of Puerto Rico (18°27′ N, 66°10′ W; Fig. 1). Annual rainfall averages 160 cm and is moderately seasonal in distribution, with wetter months occurring between July and December, and a dry season from February to June during which mean monthly rainfall usually averages <10 cm for 2–4 months. Average daily temperatures range from 24.7°C in January to 27.9°C in August.

The soils are well-drained, calcareous sands of marine origin (isohyperthermic typic troposamments) with a pH 7.0–8.0. Formerly supporting coastal dune forest vegetation, the site has been subject to frequent and often intense disturbance for at least a century, including forest clearing, sugarcane cultivation, cattle grazing, topsoil removal, and periodic fires. At the time of experimental plantation establishment, the site was dominated by grasses (mainly *Panicum maximum* and *Sporobolus jacquemontii*) and about 30 species of herbs and vines (Parrotta, 1993a); woody plants were absent. The surrounding landscape is dominated by residential housing and commercial and industrial facilities; secondary forest vegetation includes about 20 native and naturalized tree species restricted mainly to roadsides and backyards.

Experimental plantations were established in September 1989 using a randomized complete block design (Fig. 1) that included three replicate 16×16 m^2 plots of each of the following treatments:

(i) *Casuarina equisetifolia*;
(ii) *Eucalyptus x robusta*;
(iii) *Leucaena leucocephala*;
(iv) *Casuarina* + *Eucalyptus* (50 : 50);
(v) *Eucalyptus* + *Leucaena* (50 : 50);
(vi) *Casuarina* + *Leucaena* (50 : 50); and
(vii) unplanted control.

Planting stock consisted of containerized seedlings 30–60 cm in height; both *Casuarina* and *Leucaena* seedlings were well nodulated with their N_2-fixing root symbionts at the time of outplanting, having been treated with multistrain inocula of *Frankia* and *Rhizobium* in the nursery (Parrotta et al., 1994a, b). Site preparation for all plantation and control plots consisted of disk harrowing to a depth of ≈20 cm. Initial tree spacing within plantations was 1×1 m^2; in the mixed-species treatments, trees were planted in a checkerboard pattern.

2.2. Tree growth, biomass and litterfall measurements

Tree growth was monitored throughout the study period to estimate mean stem diameter, height, and basal area for each species in all treatments. During the first two years, stem basal diameters and tree heights were measured in the central $12 \times 12\ m^2$ area of each plot, excluding the outer two tree rows. Thereafter, additional buffer rows were excluded; from three years onward, trees within the central 8- $\times$ 8 m^2 were measured to calculate plot mean values for stem basal diameter, tree basal area, and tree height.

Total tree biomass and its distribution among above- and belowground components were calculated for each species in each plot at selected intervals up to four years, using biomass regressions that relate total and component-wise dry mass to stem basal diameter and height. These regressions were based on whole-tree harvests of selected individuals at 1.5 and 3.5 years representing the full range of tree sizes present in each treatment for all species. For *Casuarina*, *Eucalyptus*, and *Leucaena*, a total of 39, 42, and 31 trees were harvested, respectively; complete root systems were excavated for 18 trees of each species. Each harvested tree was separated in the field into the following biomass components: leaves (or *Casuarina* branchlets <2 mm diameter), branch or stem segments $\leq$2.5 and $\geq$2.5 cm diameter, dead branches, roots 0.2–1.0 cm in diameter, and roots >1.0 cm in diameter. Each biomass component was weighed in the field, and a random subsample was taken and oven-dried to constant weight at 65°C to yield conversion factors used to calculate tree biomass on a dry-weight basis, and to develop biomass regressions (Table 1). These subsamples were subsequently used for nutrient analyses.

Fine (<2 mm diameter) root biomass was estimated in all plantation and control plots on an annual basis during the first four years of the study from 5.1-cm diameter core samples ($n = 5$ cores/plot) taken at 10-cm intervals to a depth of 40 cm. After air-drying, soils were passed through a 1.0 mm sieve, the organic matter retained by the sieve washed with distilled water, and all roots <2 mm in diameter were extracted and oven-dried to constant weight at 65°C. Estimates of standing (forest floor) litter dry mass at 3.0 and 4.5 years were based on collection of all leaf, wood, and bark litter retained by a 1.0 mm sieve from four 0.25 m^2 quadrats, randomly located within each plot at each sampling date.

Herbaceous biomass and litter were measured in the unplanted control plots at four years in four randomly located 1-m^2 quadrats in each plot. All grasses and vines were clipped at ground level, oven-dried at 65°C to constant weight; subsamples of each component were subsequently used for nutrient analyses. Litter sampling within quadrats followed the methods described above.

Litter production was measured in each plantation plot between 1.5 and 3.5 years. At bi-weekly intervals during this period, litter was collected from four 0.25 m^2 litter traps (baskets constructed of fine-mesh plastic screen) located in each plot. Leaf litter and woody debris collected from each basket was separated by species, and dried at 70°C. Composite samples for each plot and species, comprising litter collected over 4–6-month periods, were used for nutrient analyses and subsequent calculations of total nutrient fluxes over the two-year study period.

2.3. Estimation of total biomass nutrient pools and litterfall nutrient fluxes

Aboveground biomass, litter, forest floor, and root samples were oven-dried to constant weight at 65°C and ground with a Wiley mill through a 0.85 mm (20 mesh) stainless steel sieve prior to analysis. Ground material was analyzed for P, K, Ca, Mg, Mn, Na, Al, and Fe with a Beckman Spectra Span V plasma emission spectrometer using the digestion method (concentrated HNO_3 and 30% H_2O_2), as recommended by Luh Huang and Schulte (1985). Nitrogen was analyzed using the semi-micro Kjeldahl procedure (Chapman and Pratt, 1979) involving digestion with concentrated H_2SO_4 and a catalytic mixture of $CuSO_4$ and K_2SO_4. Total C was determined by mass spectroscopy using a Leco CNS 2000 Analyzer.

The total nutrient content of aboveground biomass, roots, and litter were estimated on a unit-area basis at four years for each species in each treatment as the sum of the products of estimated biomass (by component) and their respective nutrient concentrations.

Table 1
Regression equations used to estimate tree dry mass in plantation stands up-based to four years, based on whole-tree harvests at 1.5 and 3.5 years

Biomass component	Regression[a]	r^2	d.f.	F	p
Casuarina equisetifolia					
foliage	$y = 0.156 + 0.019D_b^2$	0.639	38	65	0.0001
wood + bark <2.5 cm[b]	$y = -0.150 + 0.025D_b^2$	0.735	38	103	0.0001
wood + bark >2.5 cm	$y = -3.579 + 0.210D_b^2$	0.962	38	925	0.0001
dead wood	$y = -0.127 + 0.080D_b$	0.352	38	20	0.0001
all wood + bark	$y = -3.548 + 0.240D_b^2$	0.970	38	1195	0.0001
total aboveground biomass	$y = -3.356 + 0.260D_b^2$	0.973	38	1317	0.0001
total roots	$y = -0.551 + 0.045D_b^2$	0.774	17	55	0.0001
total tree biomass	$y = -4.190 + 0.307D_b^2$	0.961	17	393	0.0001
Eucalyptus robusta					
foliage	$y = 0.037 + 0.015D_b^2$	0.692	39	85	0.0001
wood + bark <2.5 cm	$y = 0.005 + 0.015D_b^2$	0.781	41	143	0.0001
wood + bark >2.5 cm	$y = -0.108 + 0.010D_b^2H$	0.890	39	306	0.0001
dead wood	$y = 0.270 + 0.00034D_b^2H$	0.228	41	12	0.0014
all wood + bark	$y = 0.451 + 0.011D_b^2H$	0.797	42	161	0.0001
total aboveground biomass	$y = 0.754 + 0.012D_b^2H$	0.788	42	152	0.0001
total roots	$y = -0.664 + 0.318D_b$	0.838	16	78	0.0001
total tree biomass	$y = 0.502 + 0.017D_b^2H$	0.981	16	793	0.0001
Leucaena leucocephala					
foliage	$y = -0.122 + 0.067D_b$	0.265	24	8	0.0085
wood + bark <2.5 cm	$y = 0.017 + 0.108D_b$	0.339	30	15	0.0006
wood + bark >2.5 cm	$y = -0.411 + 0.016D_b^2H$	0.943	30	478	0.0001
all wood + bark	$y = 0.061 + 0.017D_b^2H$	0.940	30	454	0.0001
total aboveground biomass	$y = 0.236 + 0.017D_b^2H$	0.938	30	436	0.0001
total roots	$y = -0.583 + 0.294D_b$	0.749	19	54	0.0001
total tree biomass	$y = 0.094 + 0.019D_b^2H$	0.915	19	193	0.0001

[a] All models tested were linear, using D_b, D_b^2, and D_b^2H as independent variables, where D_b = stem basal diameter and H = tree height; y = dry mass, in kg.
[b] Branch (or stem) diameter.

Nutrient removal rates (for N, P, K, Ca, and Mg) associated with different biomass harvest options (total aboveground biomass and stem + branch-only removal), were calculated for all treatments at four years, as the ratio of total aboveground biomass (Mg ha^{-1}) to biomass nutrient content (kg nutrient Mg^{-1} biomass).

The total nutrient content of litterfall over the two-year (1.5–3.5 years) sampling interval was calculated for each species in each plot as the mass-weighted average nutrient concentration times the total dry mass of litterfall over that period. Retranslocation of nitrogen, phosphorus and potassium prior to leaf-fall was estimated for each species and treatment by comparing mass-weighted average leaf litter nutrient concentrations over the two-year period with those of fresh leaves collected during whole-tree biomass sampling at the beginning and end of this period.

2.4. Soils

Soils were sampled to a depth of 40 cm in all plantation and control plots at 0.8 year, 3.5 years and 7.5 years using a 5.1 cm diameter core sampler (n = 5 cores/plot) taken at 10-cm intervals. After air-drying at 65°C, soils were passed through a 2.0 mm (20 mesh) sieve to remove roots prior to chemical analyses. An additional set of samples were taken at the first two sampling dates for bulk density determinations.

Soil pH was determined using an Orion Ionalyzer Model 901 pH meter in a 1 : 1 soil : water solution.

Soil organic matter was determined using the modified Walkley–Black method (Page, 1982). Total C, N, and S were determined by mass spectroscopy using a Leco CNS 2000 Analyzer. Total N was also determined using the modified Kjeldhal method to include nitrate and nitrite (Keeney and Nelson, 1982) for soils collected at 3.5 years. Exchangeable ions were determined using a Beckman Direct Current Plasma–Atomic Emission Spectrometer (SpectraSpan V) following a 1 N KCl extraction for Ca, Mg, Na and Al, and the Olsen–EDTA (NH_4–EDTA–$NaHCO_3$) extraction for P, K, Mn, and Fe (Hunter, 1974).

2.5. Understory forest regeneration

The floristic composition of plantation understory and control plots was monitored 1.0, 2.5, 4.5 and 8.5 years after plantation establishment. The total sample area per plot was 16 m^2 up to 2.5 year, 121 m^2 at 4.5 years and 100 m^2 at 8.5 years, the central zone of each plot being used for all dates. For secondary-forest tree and shrub species, all seedlings and saplings were counted and their heights recorded. These species were also classified by their primary mode of seed dispersal which, for species encountered at this site, includes dispersal by bats, birds, and wind. At 8.5 years, litter depth was measured at 10 randomly selected points per plot and mean values calculated.

2.6. Statistical analyses

One-way analyses of variance (ANOVA) were used to compare tree growth, soil chemical properties, and understory regeneration data among experimental treatments. Fisher's Protected Least Significant Difference (PLSD) procedure was used to separate the means of dependent variables which were significantly affected by treatment. Understory seedling density were evaluated in relation to overstory composition and litter depth through regression analysis.

3. Results

3.1. Tree growth and biomass yield

Tree growth rates for all species in all treatments was rapid during the first four years, and declined markedly thereafter. Mean annual stem diameter growth peaked at 2.0–3.0 years for *Leucaena* and *Eucalyptus* and at 2.5–3.5 years for *Casuarina* (Fig. 2(a–c)). For *Leucaena*, stem basal diameter treatment means ranged from 5.8 to 7.6 cm at four years and from 7.5 to 8.0 cm at 7.5 years; treatment means were not significantly different throughout this period (ANOVA; $p < .05$). *Eucalyptus* stem diameters averaged 10.0–11.0 cm at four years, and 12.9–14.0 cm at 7.5 years, with no significant differences among treatments. Mean stem diameters in *Casuarina* ranged from 7.7 to 10.0 cm at four years, and were significantly greater in the mixed stands with *Eucalyptus* than in the pure stands; at 7.5 years, treatment means ranged from 11.4 to 14.0 cm, with no significant differences among treatments. Mean tree heights at four years ranged from 8.4 to 9.7 m, 9.4 to 10.9 m, and 9.7 to 12.0 m among *Leucaena*, *Eucalyptus*, and *Casuarina* treatments, respectively (Fig. 3(a–c)). At this age, both species in the mixed *Eucalyptus*–*Casuarina* stands were significantly taller than either species in single-species stands ($p < .05$; Fisher's PLSD).

The observed differences in tree height and stem diameter growth were mainly due to differential mortality for *Casuarina* and *Eucalyptus* among single- and mixed-species treatments. Self-thinning in these, initially very dense, stands resulted in proportionately greater mortality of smaller, suppressed trees, thus increasing mean stem diameter and height values. As shown in Fig. 4, tree survival in *Casuarina* declined sharply after three years, particularly in the mixed stands with *Eucalyptus*. Similarly, *Eucalyptus* survival, which declined steadily in all treatments throughout the study, was consistently lower in the mixed-species than in the single-species stands from four years onward. *Leucaena* survival was high (>90%) in all treatments up to four years, and declined thereafter, particularly in the mixed stands with *Casuarina*.

The overall impact of differential diameter growth and mortality in single- and mixed-species stands are reflected in stand basal-area trends. As shown in Fig. 5, total basal-area development was remarkably similar among all treatments, increasing to $\approx$40 m^2 ha^{-1} at 3–4 years and remaining more or less constant thereafter, with no significant differences among treatment means throughout the study period.

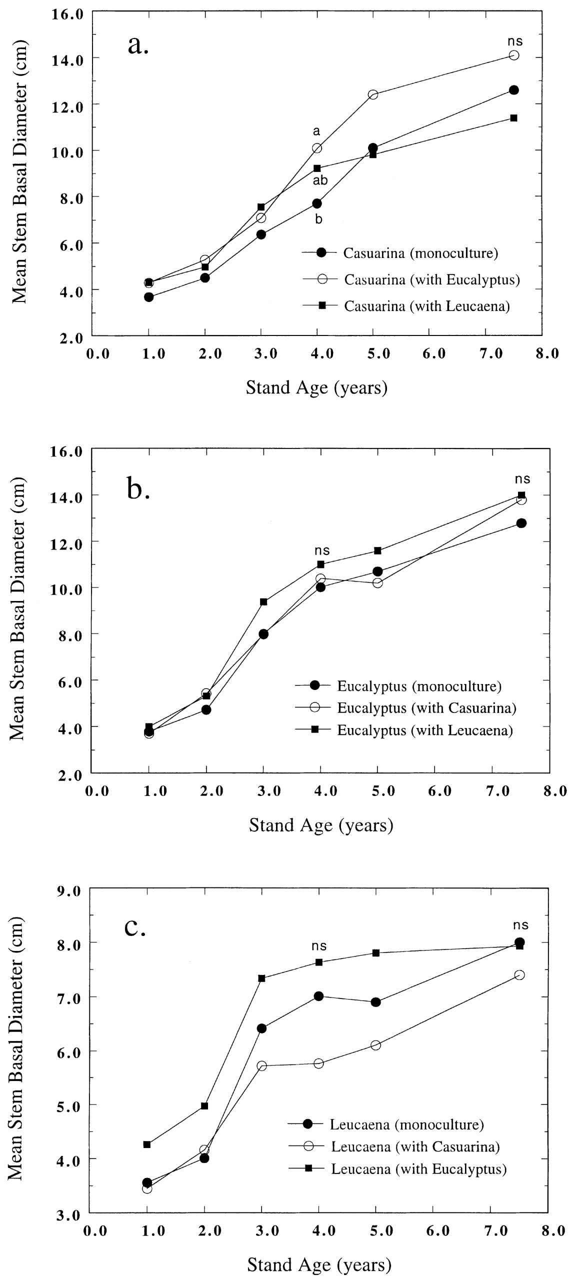

Fig. 2. Mean stem basal diameters for *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in single- and mixed-species stands to 7.5 years. Similar letters indicate that treatment means were not significantly different; ns indicates that all treatment means were similar ($p < .05$; Fisher's PLSD). $n = 3$ plots/treatment. (a) *Casuarina*; (b) *Eucalyptus*; and (c) *Leucaena*.

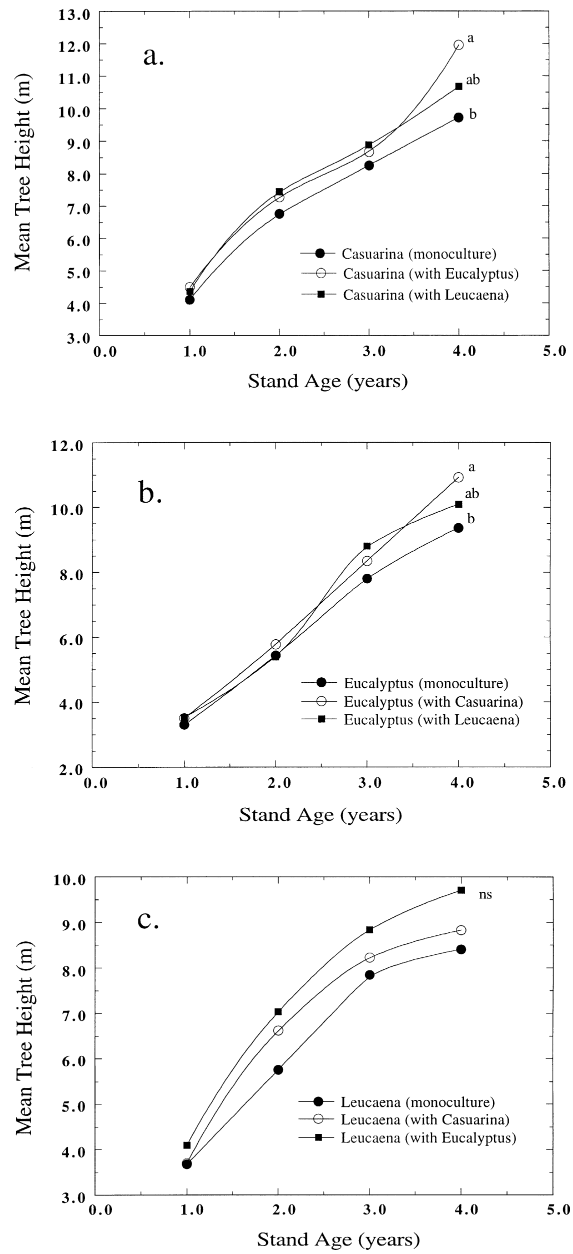

Fig. 3. Mean tree heights for *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in single- and mixed-species stands to 4.0 years. Similar letters indicate that treatment means were not significantly different; ns indicates that all treatment means were similar (p <0.5; Fisher's PLSD). $n = 3$ plots/treatment; (a) *Casuarina*; (b) *Eucalyptus*; and (c) *Leucaena*.

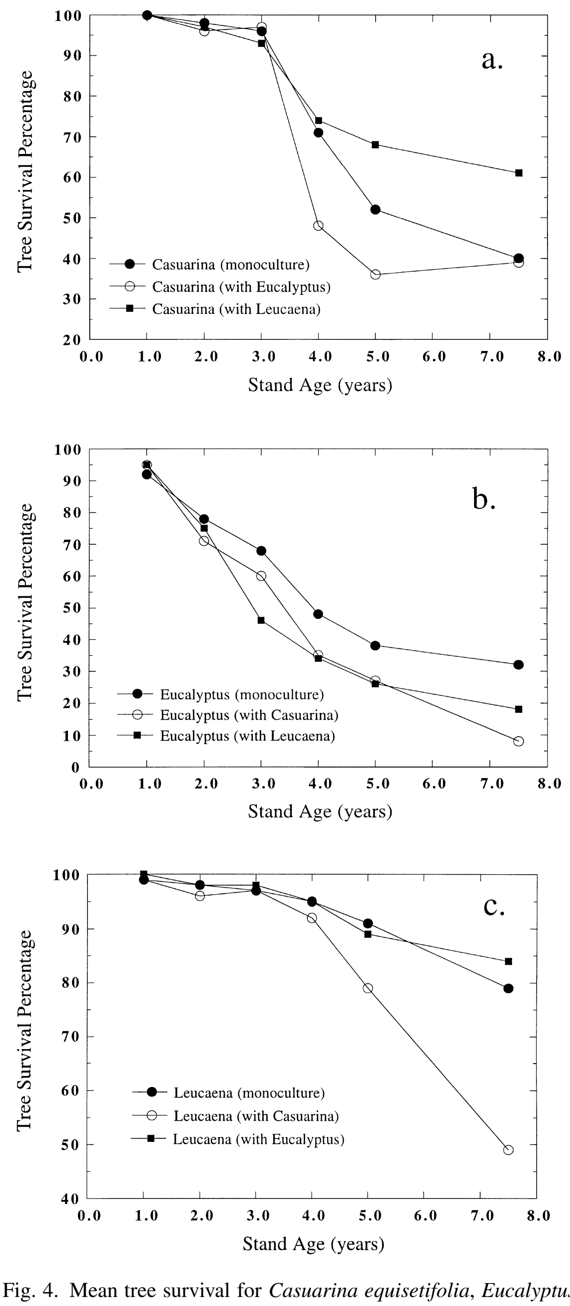

Fig. 4. Mean tree survival for *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in single- and mixed-species stands to 7.5 years. Similar letters indicate that treatment means were not significantly different; ns indicates that all treatment means were similar ($p < .05$; Fisher's PLSD). $n = 3$ plots/treatment; (a) *Casuarina*; (b) *Eucalyptus*; and (c) *Leucaena*.

What is apparent in the mixed-species treatments is the increasing dominance of *Casuarina* over both *Eucalyptus* and *Leucaena* (Fig. 5(b,c)) and, to a lesser extent, of *Leucaena* over *Eucalyptus*. In the case of the mixed-species stands with *Casuarina*, the declining basal area of *Eucalyptus* and *Leucaena* after three years indicates the competitive advantage of *Casuarina* on this site and the gradual suppression of the associated species. A somewhat different situation exists in the *Eucalyptus-Leucaena* mixture where, following peak basal area development at ≈3–4 years, no further increase or decrease in basal area is apparent for either species.

Estimated mean aboveground and whole-tree biomass were significantly different among treatments ($p < .001$; ANOVA) at four years (Table 2). Total (whole-tree) biomass ranged from 78.6 to 147.9 Mg ha^{-1} and aboveground biomass from 62.5 to 123.9 Mg ha^{-1} (or 80–87% of total biomass) among treatments. Although treatment means were generally greater in the mixed-species than in single-species stands, aboveground and total biomass estimates were significantly higher only in the *Casuarina*/*Leucaena* mixed-species treatment than in the pure stands of *Eucalyptus*. Overall, differences among treatments were due primarily to the presence or absence of *Casuarina*, which was 47–64% more productive than *Eucalyptus* and *Leucaena* in the single-species stands, and 156–168% more productive than its associated species in the mixed-species stands, based on total biomass estimates.

Total root biomass to 40 cm depth ranged from 15.1 to 24.0 Mg ha^{-1} and followed similar trends among treatments, with generally higher mean values in stands that included *Casuarina*. Fine root (<2 mm diameter) dry mass at four years averaged 4.4 Mg ha^{-1} (range of means: 2.9–5.3 Mg ha^{-1}) among plantations treatments and 5.4 Mg ha^{-1} in the unplanted control. In contrast to the unplanted control plots, which exhibited a steady increase in fine root mass over time (2.0 Mg ha^{-1}, 3.2 Mg ha^{-1}, 3.5 Mg ha^{-1} at one, two, and three years, respectively), average fine-root mass in the plantation plots increased only slightly following rapid development during the first year, at the end of which treatment means ranged from 3.4 to 5.7 Mg ha^{-1}. All treatments exhibited similar decreases in fine-root mass with depth: the percentage of total fine-root

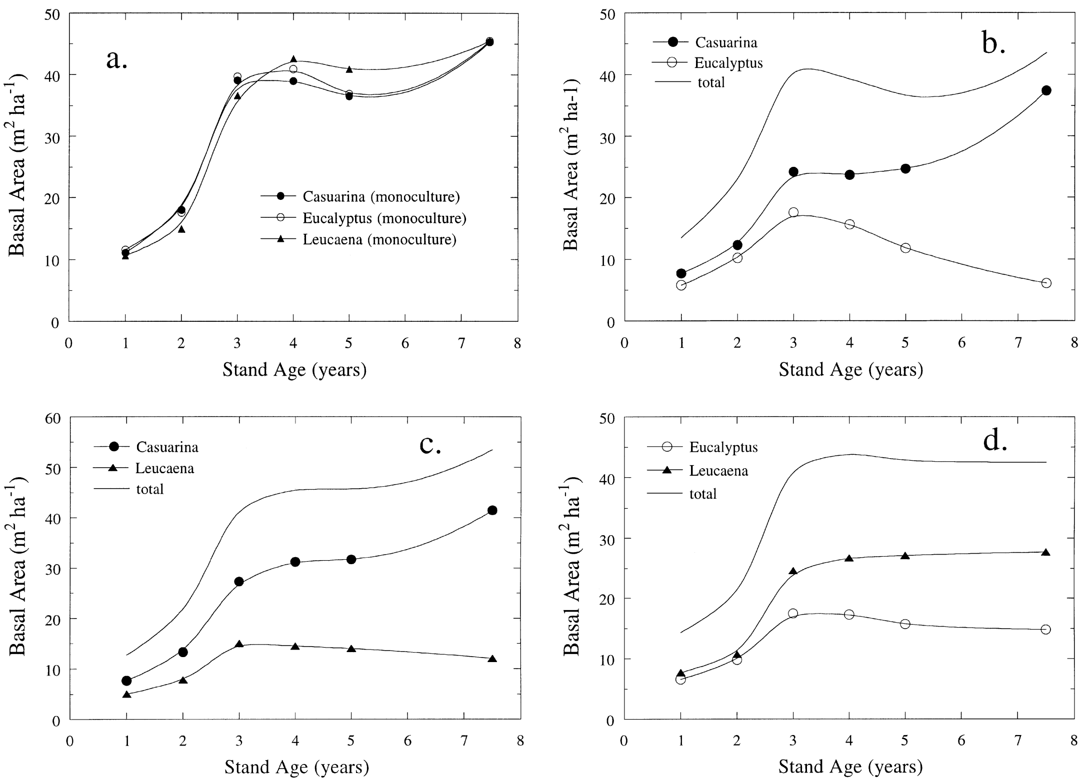

Fig. 5. Mean basal area for *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in single- and mixed-species stands to 7.5 years. $n = 3$ plots/treatment. (a) Single-species treatments; (b) *Casuarina* + *Eucalyptus*; (c) *Casuarina* + *Leucaena*; and (d) *Eucalyptus* + *Leucaena*.

mass averaged 55 ± 5 (S.E.) from 0–10 cm, 22 ± 2% from 10–20 cm, 16 ± 4% from 20–30 cm, and 7 ± 1% from 30–40 cm at four years.

Eucalyptus aboveground biomass in the mixed-species treatments was 43–50% of that in the pure *Eucalyptus* stands, or approximately equal to expected values since the planting density of each species in the mixed stands was 50% of that in the pure stands. For *Leucaena*, aboveground biomass was 47% (in mixed stands with *Eucalyptus*) and 96% (in mixed stands with *Casuarina*) of that in the pure *Leucaena* stands, suggesting that while *Eucalyptus* had no effect on *Leucaena* biomass yield, admixture with *Casuarina* resulted in a twofold increase in *Leucaena* yield relative to the pure stands. In the case of *Casuarina*, aboveground biomass was 66% (in mixed stands with *Eucalyptus*) and 86% (in mixed stands with *Leucaena*) of that in the pure *Casuarina* stands.

3.2. Litterfall production, nutrient content, and nutrient fluxes

Litterfall production, measured over a two-year period from 1.5 to 3.5 years, ranged from 5.4 to 10.0 Mg ha^{-1} year^{-1} among plantation treatments, equivalent to 22–31% of net aboveground primary production (NPP$_{ag}$) (Table 3). Leaves (or branchlets, in *Casuarina*) comprised 99.3–99.8% of total litterfall across all treatments. Among the single-species treatments, litterfall production was highest in *Leucaena* (9.7 Mg ha^{-1} year^{-1}; 31% NPP$_{ag}$), intermediate in *Casuarina* (8.6 Mg ha^{-1} year^{-1}; 22% NPP$_{ag}$) and lowest in *Eucalyptus* (5.4 Mg ha^{-1} year^{-1}; 24% NPP$_{ag}$). In the mixed-species treatments, litterfall production was generally intermediate between those of the single-species treatments: 7.7 Mg ha^{-1} year^{-1} (23% NPP$_{ag}$) in *Casuarina*/*Eucalyptus*, 8.9 Mg ha^{-1} year^{-1} (24% NPP$_{ag}$) in *Eucalyptus*/*Leucaena*, and

Table 2
Estimated biomass in four-year-old single- and mixed-species plantation of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala*. All values in Mg ha^{-1}[a]

Biomass component	*Casuarina equisetifolia*	*Eucalyptus robusta*	*Leucaena leucocephala*	*Casuarina* + *Eucalyptus*		*Casuarina* + *Leucaena*		*Eucalyptus* + *Leucaena*		Unplanted control
Foliage	13.1	7.1	2.5	7.2	2.8	9.4	1.2	3.2	1.8	0
Branches/stems										
<2.5 cm diameter	11.0	7.0	5.4	7.1	2.8	9.2	2.9	3.1	3.9	0
>2.5 cm diameter	77.9	45.6	63.9	53.4	20.4	69.3	29.6	23.8	63.3	0
Dead wood	3.2	2.8	0	1.8	1.1	2.2	0	1.3	0	0
Grasses and herbs[b]	n.a.[b]	n.a.[b]	n.a.[b]	n.a.[b]		n.a.[b]		n.a.[b]		3.1
Total aboveground	105.3ab	62.5c	71.8bc	96.5abc		123.9a		100.3abc		3.1
Roots <2 mm	5.2	4.8	5.3	4.9		3.3		2.9		5.4
Roots >2 mm	18.4	11.3	10.3	12.1	4.4	15.7	5	4.6	7.6	0
Total belowground	23.6a	16.1b	15.6b	21.4ab		24.0a		15.1b		5.4
Total biomass	128.9ab	78.6b	87.4b	117.9ab		147.9a		115.4ab		8.5

[a] ANOVA results: plantation treatment effects for aboveground, belowground, and total biomass significant at $p < .01$. Similar letters within a row indicate that means were similar ($p < .05$; Fisher's PLSD).

[b] Data not available for plantation understory vegetation.

Table 3
Litterfall production, nutrient fluxes and retranslocation in 1.5–3.5-year-old plantation stands.

	Casuarina equisetifolia	*Eucalyptus robusta*	*Leucaena leucocephala*	*Casuarina + Eucalyptus*			*Casuarina + Leucaena*			*Eucalyptus + Leucaena*			ANOVA[b]
				Casuarina	*Eucalyptus*	total	*Casuarina*	*Leucaena*	total	*Eucalyptus*	*Leucaena*	total	
Litterfall production (Mg ha^{-1} year^{-1})	8.61ab	5.42c	9.69a	*5.13*	*2.61*	7.74b	*6.69*	*3.29*	9.98 a	*2.72*	*6.15*	8.87ab	**
Aboveground NPP[a], 1.5–3.5 year (Mg ha^{-1} year^{-1})	38.5	22.4	30.9	*24.3*	*9.6*	*33.8*	*32.7*	*13.2*	*45.9*	*10.9*	*26.6*	37.5	
Litterfall percent aboveground NPP	22.4	24.2	31.4	*21.1*	*27.2*	22.9	*20.5*	*24.9*	21.7	*25.0*	*23.1*	23.7	
Litter (forest floor) at 3 year (Mg ha^{-1})	7.69	7.08	6.29	*3.79*	*1.70*	5.50			5.22	*1.72*	*3.09*	4.82	
Litter/litterfall production (%)	89	131	65	*74*	*65*	71			52	*63*	*50*	54	
Litterfall nutrient flux (kg ha^{-1} year^{-1})													
carbon	3810ab	2390c	4180a	*2280*	*1280*	3560b	*1230*	*3210*	4435a	*1280*	*2650*	3930ab	**
nitrogen	105.0b	42.2c	193.4a	*56.6*	*26.7*	83.3bc	*45.1*	*117.7*	162.8a	*26.7*	*142.0*	168.7a	***
phosphorus	2.16b	1.10b	4.54a	*1.07*	*0.77*	1.84b	*1.05*	*2.74*	3.79a	*0.77*	*3.77*	4.54a	**
potassium	24.9a	14.5b	33.1a	*12.1*	*9.4*	21.5a	*8.4*	*22.0*	30.4a	*9.4*	*24.2*	33.6a	n.s.
aluminum	2.08ab	0.84b	1.93ab	*1.39*	*0.51*	1.90ab	*0.84*	*2.18*	3.02a	*0.51*	*1.67*	2.18ab	n.s.
calcium	124.0c	84.9c	281.0a	*78.2*	*37.8*	116.0c	*59.5*	*155.2*	214.7b	*37.8*	*154.4*	192.2b	***
iron	2.77ab	0.96b	2.95ab	*1.70*	*0.60*	2.30ab	*1.12*	*2.91*	4.03a	*0.60*	*2.26*	2.86ab	n.s.
magnesium	21.9c	17.4c	51.1a	*11.4*	*9.8*	21.2c	*9.5*	*24.7*	34.2b	*9.8*	*31.9*	41.7b	***
manganese	0.77ab	1.01a	0.63b	*0.53*	*0.41*	0.94ab	*0.27*	*0.70*	0.97b	*0.41*	*0.49*	0.90ab	n.s.
sodium	19.9a	9.0a	14.5a	*16.8*	*7.3*	24.1a	*8.8*	*22.9*	31.7a	*7.3*	*16.1*	23.4a	n.s.
Percent retranslocation[c]													
nitrogen	30c	48a	38abc	34bc	50ab		46abc	42abc		27c	40abc		n.s.
Phosphorus	54ab	66a	52ab	63ab	68a		69a	45b		51ab	56ab		n.s.
potassium	52cd	56bc	68a	57bc	55c		38e	76a		43de	66ab		***

[a] Calculated as annual average of litterfall dry mass plus standing biomass increment between 1.5 and 3.5 years.
[b] ANOVA results: n.s. – treatment effect not significant; * – $p < 0.05$; ** – $p < 0.01$; *** – $p < 0.001$. Similar letters within a row indicate that means were similar ($p < 0.05$; Fisher's PLSD).
[c] Calculated as: [1 − (weighted average leaf litter nutrient concentration$_{t1.5–3.5}$/mean live leaf nutrient concentration$_{t1.5,\ 3.5\ \text{tree harvest samples}}$)] × 100.

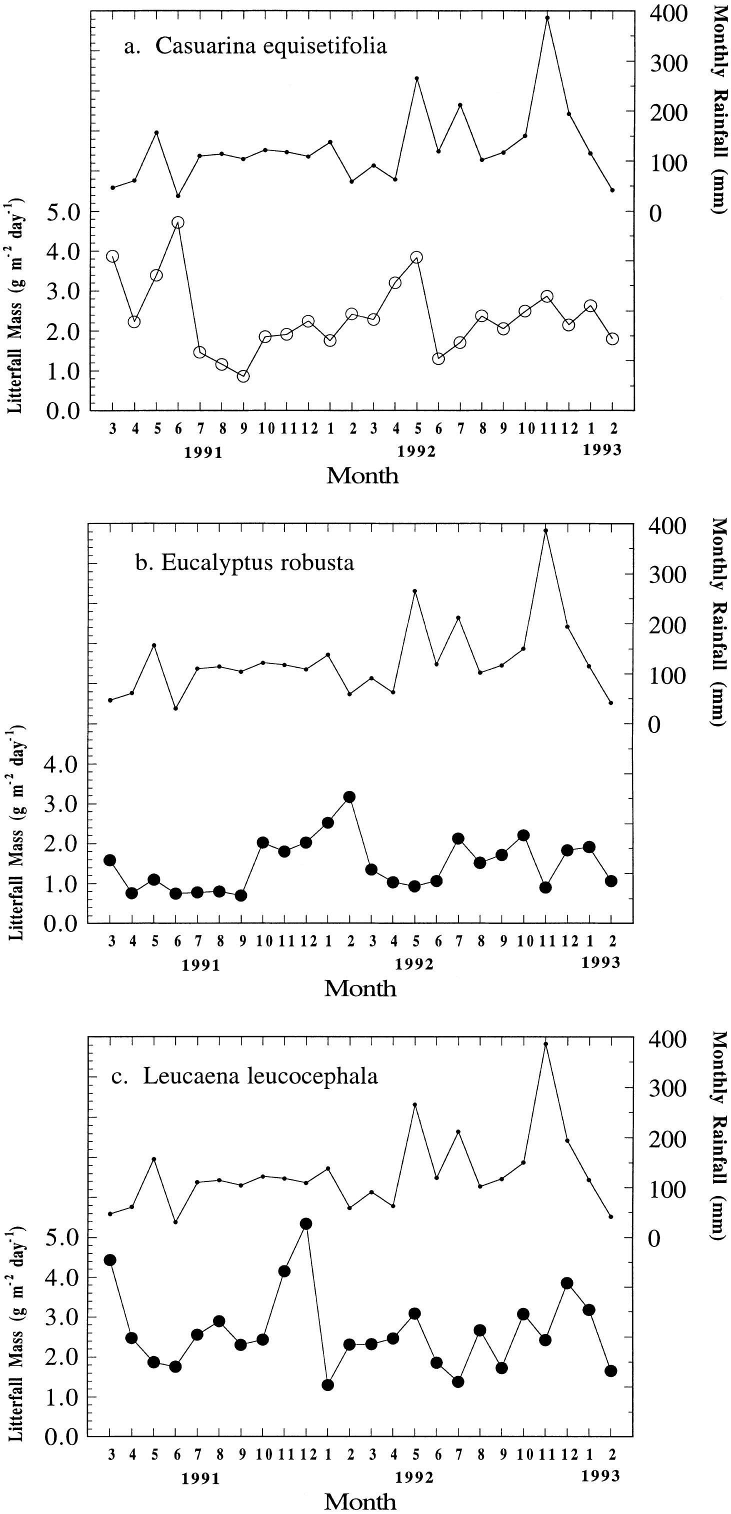

Fig. 6. Average monthly litterfall dry mass in 1.5–3.5-year-old single- and mixed-species stands of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala*. (a) *Casuarina* monoculture; (b) *Eucalyptus* monoculture; (c) *Leucaena* monoculture; (d) *Casuarina* + *Eucalyptus*; (e) *Casuarina* + *Leucaena*; and (f) *Eucalyptus* + *Leucaena*.

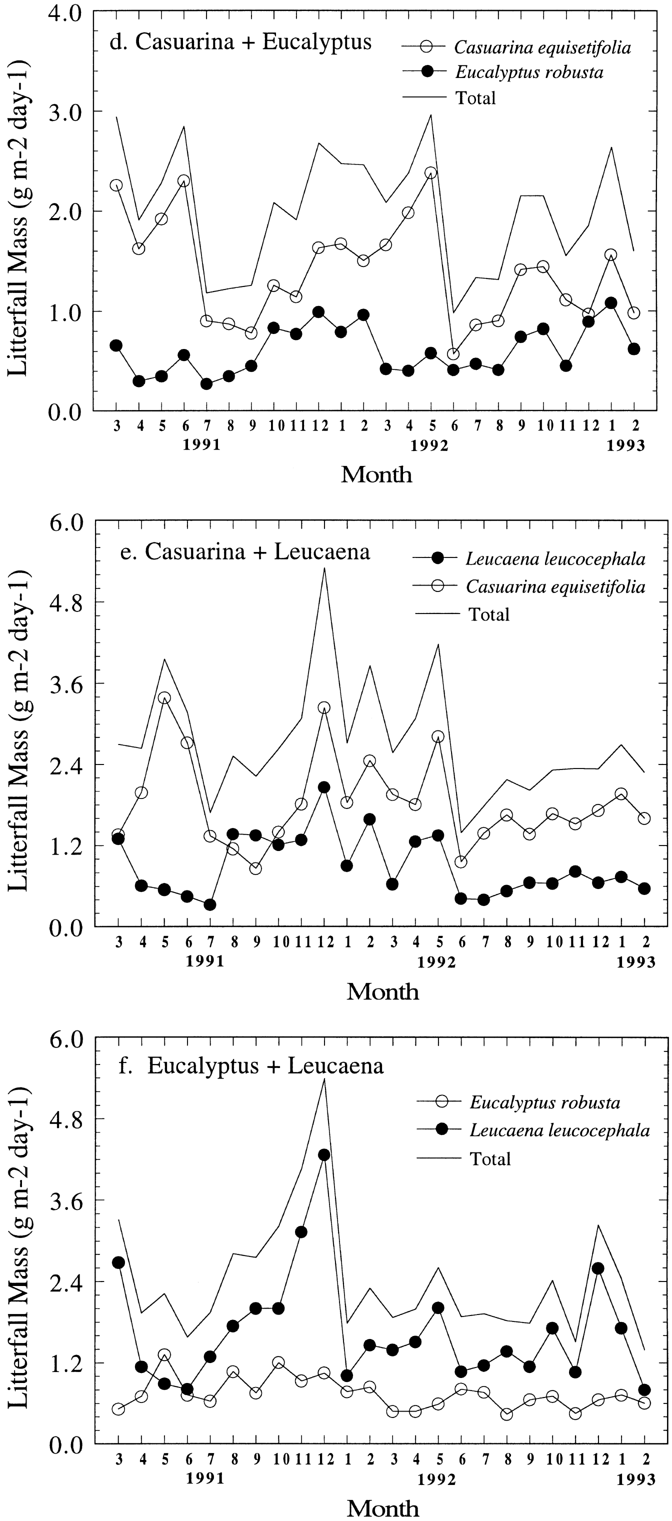

Fig. 6. (*Continued*)

Table 4
Biomass and litter nutrient concentrations. All values expressed on an ash-free dry weight basis

	Casuarina equisetifolia	*Eucalyptus robusta*	*Leucaena leucocephala*	*Casuarina + Eucalyptus*		*Casuarina + Leucaena*		*Eucalyptus + Leucaena*	
Total aboveground biomass									
carbon (mg/g)	458	469	451	455	454	451	454	450	456
nitrogen (mg/g)	5.6	4.5	9.3	4.6	4.8	4.7	8.0	4.1	8.0
phosphorus (mg/g)	0.145	0.315	0.244	0.134	0.299	0.125	0.249	0.240	0.271
potassium (mg/g)	2.09	2.78	4.12	1.71	2.14	1.75	4.27	2.14	3.45
calcium (mg/g)	8.0	16.0	12.5	7.5	13.2	6.5	10.9	12.8	10.1
magnesium (mg/g)	0.63	1.64	1.35	0.60	2.04	0.60	1.32	1.76	1.30
manganese (mg/g)	0.035	0.123	0.008	0.024	0.074	0.039	0.006	0.067	0.013
aluminum (mg/g)	0.041	0.040	0.026	0.050	0.081	0.033	0.030	0.064	0.097
iron (mg/g)	0.109	0.067	0.068	0.061	0.077	0.058	0.053	0.214	0.138
sodium (mg/g)	0.47	0.56	0.14	0.66	1.10	0.37	0.17	0.98	0.32
Leaves									
carbon (mg/g)	438	444	416	442	432	430	437	442	443
nitrogen (mg/g)	18.1	15.1	33.2	17.3	14.6	16.5	38.4	14.9	39.0
phosphorus (mg/g)	0.562	0.615	0.996	0.570	0.587	0.531	1.184	0.642	1.410
potassium (mg/g)	6.23	6.08	10.92	5.59	6.07	5.84	13.37	6.56	11.69
calcium (mg/g)	11.6	11.7	29.5	10.9	9.5	11.1	15.5	12.2	14.8
magnesium (mg/g)	2.40	2.30	4.79	2.26	3.83	2.56	4.41	3.74	4.35
manganese (mg/g)	0.066	0.106	0.042	0.047	0.134	0.063	0.041	0.156	0.043
aluminum (mg/g)	0.160	0.088	0.083	0.188	0.119	0.184	0.083	0.094	0.102
iron (mg/g)	0.219	0.096	0.202	0.226	0.161	0.250	0.196	0.134	0.119
sodium (mg/g)	3.28	2.38	1.33	4.06	2.58	2.86	0.99	2.61	1.45
Branches and stems <2.5 cm diameter									
carbon (mg/g)	458	549	439	455	450	461	441	444	445
nitrogen (mg/g)	6.1	4.9	13.3	5.0	5.0	4.9	11.3	4.4	12.7
phosphorus (mg/g)	0.165	0.411	0.426	0.162	0.428	0.132	0.482	0.421	0.568
potassium (mg/g)	2.29	5.25	9.14	1.99	2.41	1.93	9.55	2.71	9.78
Calcium (mg/g)	9.3	18.2	15.6	10.7	15.7	7.9	16.8	17.0	17.9
magnesium (mg/g)	0.70	2.52	2.35	0.67	2.18	0.56	2.50	2.07	2.31
manganese (mg/g)	0.045	0.147	0.015	0.040	0.100	0.049	0.016	0.103	0.017
aluminum (mg/g)	0.033	0.039	0.040	0.049	0.031	0.030	0.143	0.056	0.114
iron (mg/g)	0.085	0.078	0.103	0.061	0.050	0.073	0.076	0.127	0.175
sodium (mg/g)	0.42	0.59	0.36	0.56	0.54	0.38	0.39	1.54	1.94
Branches and stems >2.5 cm diameter									
carbon (mg/g)	461	462	454	456	459	453	454	451	456
nitrogen (mg/g)	3.6	3.0	8.1	2.8	3.3	3.0	6.4	2.7	6.8
phosphorus (mg/g)	0.088	0.275	0.204	0.081	0.237	0.081	0.196	0.185	0.220

potassium (mg/g)	1.47	2.05	3.43	1.26	1.62	1.23	3.33	1.64	2.80
calcium (mg/g)	7.7	16.8	11.2	6.8	13.6	6.0	10.2	13.1	9.6
magnesium (mg/g)	0.28	0.17	1.13	0.30	1.72	0.29	1.09	1.43	1.15
manganese (mg/g)	0.029	0.115	0.006	0.020	0.059	0.035	0.005	0.058	0.012
aluminum (mg/g)	0.016	0.032	0.023	0.025	0.081	0.020	0.022	0.051	0.096
iron (mg/g)	0.088	0.062	0.061	0.033	0.070	0.041	0.041	0.230	0.135
sodium (mg/g)	0.21	0.44	0.07	0.25	1.05	0.17	0.12	0.67	0.18
Roots <0.2 cm diameter									
carbon (mg/g)	408	397	294		420		394		361
nitrogen (mg/g)	7.7	6.2	1.3		7.0		1.0		8.8
phosphorus (mg/g)	0.210	0.290	0.390		0.123		0.160		0.230
potassium (mg/g)	1.11	1.49	3.47		0.80		1.71		1.64
calcium (mg/g)	19.3	21.2	22.3		15.9		10.9		12.0
magnesium (mg/g)	1.62	1.96	4.44		1.41		1.71		2.56
manganese (mg/g)	0.081	0.093	0.230		0.062		0.079		0.130
aluminum (mg/g)	1.450	1.380	4.730		1.270		1.740		2.900
iron (mg/g)	2.150	2.260	7.030		1.780		2.480		4.140
sodium (mg/g)	0.60	0.63	1.15		0.63		0.81		1.08
Roots 0.2–1.0 cm diameter									
carbon (mg/g)	450	442	451	452	445	453	452	438	456
nitrogen (mg/g)	7.2	4.6	13.3	5.7	5.3	6.8	15.7	5.5	14.2
phosphorus (mg/g)	0.265	0.309	0.277	0.206	0.277	0.223	0.455	0.281	0.341
potassium (mg/g)	2.71	2.67	4.89	2.22	2.61	2.08	3.81	2.63	3.37
calcium (mg/g)	11.9	12.8	11.7	7.3	8.2	7.3	9.5	10.0	7.0
magnesium (mg/g)	1.20	1.88	1.81	0.63	1.20	0.73	1.60	2.01	1.47
manganese (mg/g)	0.051	0.060	0.043	0.029	0.045	0.033	0.036	0.055	0.033
aluminum (mg/g)	0.837	0.699	0.726	0.458	0.420	0.574	0.605	0.937	0.981
iron (mg/g)	1.293	1.018	1.035	0.659	0.692	0.775	0.977	1.251	0.631
sodium (mg/g)	1.39	0.46	2.33	0.88	1.97	1.02	2.37	1.48	1.77
Roots >1.0 cm diameter									
carbon (mg/g)	455	442	432	456	440	446	453	437	450
nitrogen (mg/g)	3.7	4.8	15.5	3.8	5.5	5.5	14.6	4.2	13.7
phosphorus (mg/g)	0.062	0.279	0.189	0.065	0.240	0.151	0.341	0.220	0.151
potassium (mg/g)	1.05	1.74	2.97	1.02	1.64	1.78	3.44	1.77	1.78
calcium (mg/g)	3.4	7.6	6.6	3.7	5.9	4.2	6.2	8.0	4.2
magnesium (mg/g)	0.35	1.22	1.20	0.37	1.07	0.69	1.25	1.15	0.68
manganese (mg/g)	0.017	0.050	0.016	0.015	0.032	0.021	0.007	0.034	0.021
aluminum (mg/g)	0.220	0.407	0.346	0.234	0.402	0.322	0.265	0.579	0.322
iron (mg/g)	0.349	0.578	0.593	0.365	0.617	0.429	0.441	0.897	0.429
sodium (mg/g)	0.39	0.68	0.22	0.24	0.74	0.34	0.60	0.81	0.34

Table 4 (*Continued*)

	Casuarina equisetifolia	*Eucalyptus robusta*	*Leucaena leucocephala*	*Casuarina + Eucalyptus*		*Casuarina + Leucaena*		*Eucalyptus + Leucaena*	
Litterfall (leaves)									
carbon (mg/g)	454	449	442	457	473	507	535	460	442
nitrogen (mg/g)	12.5	7.9	20.4	11.3	9.9	8.9	22.2	8.7	23.7
phosphorus (mg/g)	0.257	0.207	0.479	0.214	0.285	0.166	0.646	0.234	0.628
potassium (mg/g)	2.97	2.71	3.50	2.43	3.48	3.60	3.24	3.10	4.03
calcium (mg/g)	14.8	15.9	29.7	15.7	14.0	19.4	24.9	13.7	25.7
magnesium (mg/g)	2.61	3.27	5.40	2.27	3.63	2.58	4.47	3.47	5.32
manganese (mg/g)	0.091	0.189	0.067	0.106	0.152	0.091	0.071	0.148	0.081
aluminum (mg/g)	0.248	0.157	0.204	0.278	0.189	0.304	0.240	0.153	0.278
iron (mg/g)	0.329	0.181	0.311	0.34	0.223	0.478	0.402	0.175	0.376
sodium (mg/g)	2.37	1.70	1.53	3.37	2.70	6.72	3.86	2.15	2.69
Litter (A0 horizon)									
carbon (mg/g)	436	427	393		436		421		429
nitrogen (mg/g)	12.5	7.0	15.7		7.9		12.4		8.8
phosphorus (mg/g)	0.140	0.179	0.300		0.103		0.171		0.167
potassium (mg/g)	0.75	0.87	1.19		0.69		1.04		1.13
calcium (mg/g)	14.2	18.0	24.2		11.0		13.8		39.8
aluminum (mg/g)	0.989	0.560	1.470		0.461		1.193		0.703
magnesium (mg/g)	1.57	1.79	3.15		1.30		1.90		2.08
manganese (mg/g)	0.136	0.182	0.141		0.096		0.133		0.103
iron (mg/g)	4.760	0.804	2.035		0.620		1.770		1.000
sodium (mg/g)	0.73	0.32	0.45		1.89		0.78		0.72

Notes: Data for tree biomass components based on analysis of composite samples of each component from trees harvested at 3.5 year. For aboveground components, $n = 3$ trees per species for leucaena monoculture and leucaena + casuarina treatments; $n = 6$ trees per species for eucalyptus + leucaena treatment; $n = 9$ trees per species for casuarina and eucalyptus monocultures, and casuarina + eucalyptus treatments; for roots >0.2 cm diameter, $n = 3$ trees per species for all treatments.

Total aboveground biomass values are mass-weighted averages for leaves + all branches and stems (incl. bark).

For roots <0.2 cm diameter,data based on analyses of fine roots from 5.1 cm core samples (0–40 cm; $n = 5$, composited per plot) taken from each plot at 4.0 year ($n = 3$ plots/treatment).

Leaf litterfall nutrient values are weighted averages for bi-weekly collections in all plantation treatments from 1.5 to 3.5 year.

Litter (forest floor: Ao horizon) values based on analyses of composited samples from four 0.25 m^2 quadrats per plot at three years; $n = 3$ plots/treatment.

10.0 Mg ha^{-1} year^{-1} (22% NPP$_{ag}$) in the *Casuarina*/*Leucaena* treatment.

In all treatments, litterfall was highly variable during the two-year study period, and ranged from 20 to 170 g m^{-2} month^{-1} or 0.70 to 5.39 g m^{-2} day^{-1} (Fig. 6(a–f)). There were no obvious seasonal differences among species, nor could the observed litterfall fluctuations be attributed to monthly rainfall patterns. Rather, leaf production and leaf fall are more or less continuous and aseasonal in all three species. Peaks in litterfall appear to be associated with several climatic factors, including extended periods of low rainfall, heavy rainfall events, and high winds.

Leaf-litter nutrient concentrations showed marked differences both, among species and, for certain elements, within species among treatments (Table 4). For macronutrient elements (N, P, K, Ca, Mg), leaf-litter concentrations were generally higher in *Leucaena* than in either *Casuarina* or *Eucalyptus*. Average leaf-litter nitrogen concentrations in *Leucaena* ranged from 20.4 to 23.7 mg g^{-1} among treatments, from 8.9 to 12.5 mg g^{-1} in *Casuarina*, and from 7.9 to 9.9 mg g^{-1} in *Eucalyptus*. Phosphorus concentrations were also much higher in *Leucaena* (0.48–0.65 mg g^{-1}) than in *Casuarina* (0.17–0.26 mg g^{-1}) or *Eucalyptus* (0.21–0.29 mg g^{-1}). Potassium concentrations followed similar trends among species: 3.24–4.03 mg g^{-1} in *Leucaena*, 2.43–3.60 mg g^{-1} in *Casuarina*, and 2.71–3.48 mg g^{-1} in *Eucalyptus*. Similarly, calcium and magnesium concentrations were greater in *Leucaena* litter, intermediate in *Casuarina*, and lowest in *Eucalyptus*. Comparing single- and mixed-species treatments, leaf-litter macronutrient concentrations for *Casuarina* were lower in the mixed stands with *Leucaena* for N and P and higher in K, Ca, and Mg than in either of the other two treatments. *Eucalyptus* leaf-litter macronutrient concentrations were consistently higher in the mixed-species stands than in the monoculture. For *Leucaena*, leaf-litter concentrations for N, P, and K were also higher in the two mixed species than in the single-species treatment.

Significant differences ($p < .05$, Fisher's PLSD) in nutrient retranslocation. i.e. the percentage of N, P, or K withdrawn from leaves prior to leaf-fall, were observed among species and, for *Casuarina* and *Eucalyptus*, among treatments (Table 3). In *Casuarina*, N retranslocation was somewhat higher in the mixed-species stands with *Leucaena* (46%) than in the other two treatments (30–34%); P retranslocation increased from 54% in the monoculture to 69% in the mixed-species treatment with *Leucaena*; K retranslocation was significantly lower in the mixed-species stands with *Leucaena* (38%) than in the other two treatments (52–57%). Retranslocation in *Leucaena* was variable but not significantly different among treatments for N (38–42%), P (45–56%), or K (66–76%). For *Eucalyptus*, retranslocation was significantly lower in the mixed-species treatment with *Leucaena* than in the other two treatments for both, N (27% vs. 48–50%) and K (43% vs. 55–56%); no treatment effects were found for P retranslocation in *Eucalyptus*, which ranged from 51% to 69%.

Litterfall fluxes were significantly different among species and treatments for C, N, P, Ca, and Mg ($P < .05$, ANOVA; Table 3). On account of treatment differences in litter production and species differences in litter-nutrient concentrations, the *Eucalyptus* monoculture treatment had the lowest litterfall nutrient fluxes for most elements, while the highest nutrient fluxes were associated with treatments that included *Leucaena*, particularly the *Leucaena* monoculture. Nitrogen return through litterfall was significantly greater ($p < .05$, Fisher's PLSD) in stands containing *Leucaena* (169–193 kg ha^{-1} year^{-1}) than in the remaining three treatments with *Casuarina* and/or *Eucalyptus* (42–105 kg ha^{-1} year^{-1}). The same significant differences were found for phosphorus, which ranged from 1.10 to 2.16 kg ha^{-1} year^{-1} in stands comprised *Casuarina* and/or *Eucalyptus*, to 3.79–4.54 kg ha^{-1} year^{-1} in stands with *Leucaena*. Potassium return through litterfall ranged from 14.5 kg ha^{-1} year^{-1} in the *Eucalyptus* monoculture to 33.6 kg ha^{-1} year^{-1} in the *Eucalyptus*/*Leucaena* mixed-species treatments. While treatments with *Leucaena* had higher values than those without *Leucaena*, litterfall K flux rates were significantly different only between these to extreme values. Litterfall flux rates for Ca (84.9–281.0 kg ha^{-1} year^{-1} among treatments) and Mg (17.4 to 51.1 kg ha^{-1} year^{-1} among treatments) followed the same trends as for N and P, with treatments containing *Leucaena* returning significantly greater quantities of these elements than those with only *Casuarina* and/or *Eucalyptus*.

Forest floor (litter) mass at three years ranged from 4.8 to 7.7 Mg ha^{-1}, equivalent to 52–131% of mean annual litterfall (Table 3). Among the single-species treatments, the ratio of forest floor mass to mean annual litter production was lowest in *Leucaena*, intermediate in *Casuarina*, and highest in *Eucalyptus*. These data suggest that litter decomposition rates were greater in *Leucaena*, and to a lesser degree in *Casuarina*, than in *Eucalyptus*. Differences in litter quality, particularly carbon : nitrogen ratios, may help to explain these results; C : N ratios were lowest in *Leucaena* (22), intermediate in *Casuarina* (36), and highest in *Eucalyptus* (57). In the mixed-species stands, mass-weighted litterfall C : N ratios were somewhat lower than those expected from the single-species treatment values: 43 for *Casuarina/Eucalyptus*, 27 for *Casuarina/Leucaena*, and 23 for *Eucalyptus/Leucaena*. Although litterfall rates were generally higher in the mixed-species treatments, litter accumulation was lower in these treatments than in the single-species stands. These results strongly suggest that litter decomposition rates for all species were enhanced in the mixed stands relative to the single-species stands.

3.3. Soil physical and chemical properties

Despite differences in biomass productivity and nutrient return, there were very few significant ($p < .05$, Fisher's PLSD) differences in soil properties (to 40 cm depth) among experimental treatments at 7.5 years (Table 5). Bulk density, which ranged from 1.10 to 1.19 g cm^{-3}, was slightly – though not significantly – lower in the plantations than in the unplanted control plots. Soil pH, ranging from 7.08 to 7.99, was significantly reduced only in the *Eucalyptus/Leucaena* treatment relative to the control. Soil organic matter varied from 2.99% to 4.53% relative to the control plots, treatment means were higher in the mixed-species treatments and lower in the monocultures, although treatment differences were significant only between the *Casuarina/Eucalyptus* and *Eucalyptus/Leucaena* mixtures and the *Casuarina* and *Eucalyptus* monocultures ($p < .05$, Fisher's PLSD).

Total soil carbon ranged from 12.2 to 17.9 mg g^{-1} among treatments at 7.5 years and was generally – though not significantly – lower in the plantation treatments than the control. Calculated changes in soil carbon content within treatments from 0.8 to 7.5 years varied from −0.18% in the *Leucaena* monoculture to +0.38% in the *Eucalyptus/Leucaena* mixture; relative to the control treatment, however, the observed changes in soils beneath plantations were not significant.

Total nitrogen in plantation soils at 7.5 years was significantly greater in the *Casuarina/Eucalyptus* and *Eucalyptus/Leucaena* treatments (1.23–1.29 mg g^{-1}) than in the *Eucalyptus* monoculture (0.63 mg g^{-1}), although no significant differences were found between the plantation and control (0.86% mg g^{-1}) treatments ($p < .05$, Fisher's PLSD). At the start of the experiment (at 0.8 year), soils in the mixed-species treatment plots had significantly higher average N concentrations, and somewhat lower C concentrations, than those of the single-species and control treatments. Therefore, changes in soil nitrogen within treatments from 0.8 to 7.5 years are a better indicator of the possible effects of these species on soil N content. These ranged from −0.029% in the *Eucalyptus* monoculture to +0.17% in the *Leucaena* monoculture, with only very slight differences among the remaining plantation and control treatments (−0.002% to +0.007%); differences among treatments were not significant but the variances among treatment replicates were very high.

Carbon : nitrogen ratios, ranging from 9.8 to 24.7 at 0.8 year and from 11.0 to 29.0 at 7.5 years were lower in the mixed-species than single-species or control treatments at both sampling dates. Although treatment differences were not significant, there was an apparent increase in soil C : N ratios in the control and, particularly, *Eucalyptus* monoculture treatments, a decrease in the *Leucaena* monoculture treatment, and no marked change in the remaining treatments.

The data on available elements (P, K, Ca, Mg, Mn, Na, Fe and Al) at 7.5 years indicate few significant ($p < .05$, Fisher's PLSD) differences in soils plantation and control treatments. Several apparent differences in soil properties among treatments were probably due to pre-plantation site variability (Table 5). As was the case for soil organic matter and nitrogen, soils beneath the mixed-species treatments generally had higher concentrations of available K, Mg, Na, and Fe than the single-species or control treatments, and a higher effective cation exchange capacity (ECEC) than the soils beneath the monocultures. One very obvious difference between plantation and control treatments is the marked increase in available Na in the plantation

Table 5
Soil chemical properties in plantation and control plots at 0.2 and 7.5 year; 0–20 cm depth[a]

	Age (year)	Unplanted Control	*Casuarina equisetifolia*	*Eucalyptus robusta*	*Leucaena leucocephala*	*Casuarina* + *Eucalyptus*	*Casuarina* + *Leucaena*	*Eucalyptus* + *Leucaena*	ANOVA[b]
pH (1 : 1 H_2O)	0.2	7.71ab	7.82ab	7.95a	7.84ab	7.77ab	7.60ab	7.33b	ns
	7.5	7.70a	7.93a	7.77a	7.95a	7.55ab	7.79a	6.94b	ns
	change	(*0.01*)b	*0.11*ab	(*0.18*)c	*0.11*ab	(*0.22*)c	*0.19*a	(*0.39*)d	***
Organic matter (LOI)	0.2	5.04 b	5.44b	5.73ab	5.07b	6.11ab	8.09a	6.33ab	ns
	7.5	4.24 ab	3.91ab	3.58b	3.93ab	5.19a	4.57ab	5.01a	ns
	change	(*0.80*)a	(*1.52*)a	(*2.15*)a	(*1.14*)a	(*0.93*)a	(*3.52*)a	(*1.33*)a	ns
ECEC (meq/100 g)[c]	0.2	12.09c	14.36abc	13.83abc	12.87c	12.83bc	17.20a	17.00ab	ns
	7.5	9.73ab	8.34ab	6.86b	9.30ab	8.22ab	10.10a	10.08a	ns
	change	(*2.35*)a	(*6.03*)b	(*6.97*)b	(*3.56*)ab	(*4.62*)ab	(*7.10*)b	(*6.92*)b	ns
Nutrient content (kg/ha)									
Nitrogentotal	0.2	2213a	2421a	2786a	2181a	2778a	2747a	2591a	ns
	7.5	2811ab	2373ab	2035b	2663ab	3158ab	3077ab	3469a	ns
	change	*598*ab	(*48*)ab	(*752*)b	*481*ab	*380*ab	*330*ab	*878*a	ns
$Phosphorus_{available}$	0.2	13.1ab	18.8a	15.8ab	15.8ab	14.3ab	10.4b	8.9b	ns
	7.5	18.8a	14.3a	13.2a	17.8a	16.0a	15.4a	15.8a	ns
	change	*5.7*a	(*4.5*)a	(*2.4*)a	*2.0*a	*1.7*a	*5.1*a	*6.9*a	ns
$Potassium_{available}$	0.2	104a	98a	94a	108a	79ab	57b	97a	ns
	7.5	261ab	222b	224b	239ab	255ab	260ab	286a	ns
	change	*157*ab	*124*b	*130*ab	*131*ab	*176*ab	*203*a	*189*ab	ns
$Calcium_{available}$	0.2	3589c	4514abc	4308abc	3729bc	3747abc	4940a	4786ab	ns
	7.5	3733a	2610b	2360b	3054ab	2530b	3161ab	3087ab	ns
	change	*143*a	(*1875*)b	(*1948*)b	(*675*)ab	(*1217*)ab	(*1823*)b	(*1699*)b	ns
$Magnesium_{available}$	0.2	280a	291a	277a	300a	286a	403a	373a	ns
	7.5	364ab	331ab	263b	363ab	315ab	419ab	544a	ns
	change	*84*a	*40*a	(*14*)a	*63*a	*29*a	*16*a	*171*a	ns
$Sodium_{available}$	0.2	419a	420a	508a	502a	410a	423a	336a	ns
	7.5	67bc	96bc	86c	109bc	194bc	391a	242b	**
	change	(*352*)c	(*323*)c	(*422*)c	(*393*)bc	(*216*)abc	(*32*)a	(*94*)ab	*
$Manganese_{available}$	0.2	28.3ab	40.7a	30.3ab	34.3ab	27.4ab	18.6b	24.5ab	ns
	7.5	43.7a	43.8a	31.8a	41.8a	41.0a	44.6a	36.7a	ns
	change	*15.4*ab	*3.1*ab	*1.5*b	*7.5*ab	*13.6*ab	*26.0*a	*12.1*ab	ns

Table 5 (*Continued*)

	Age (year)	Unplanted Control	*Casuarina equisetifolia*	*Eucalyptus robusta*	*Leucaena leucocephala*	*Casuarina* + *Eucalyptus*	*Casuarina* + *Leucaena*	*Eucalyptus* + *Leucaena*	ANOVA[b]
$Iron_{available}$	0.2	32.4a	37.0a	21.7a	31.9a	17.7a	24.0a	38.6a	ns
	7.5	59.0ab	42.6ab	22.6b	41.3ab	70.0ab	81.4a	75.8ab	ns
	change	*26.6*abc	*5.6*bc	*0.9*c	*9.4*bc	*52.3*a	*57.4*a	*37.3*ab	*

[a] Based on five composited 5.1 cm diameter core samples per plot; $n = 3$ replicate plots per treatment. Negative values in parentheses.

[b] ANOVA results: ns – treatment effect not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Similar letters within a row indicate treatment means that were similar ($p < 0.05$; Fisher's PLSD).

[c] Effective cation exchange capacity = exchangeable Ca + Mg + Na + Al + K.

soils. This is most likely the result of increased deposition of sea salt on the foliage of the planted trees and its gradual accumulation in the soil profile; the very high Na concentrations in foliage and litter in experimental plots located closest to the seashore at this site supports this hypothesis.

3.4. System nutrient stores and harvest impacts

Total carbon, total nitrogen and available nutrient elements in biomass and soils to a depth of 40 cm (in plant available forms for cations) were markedly higher in the plantation than unplanted control plots at four years (Table 6). Aboveground and root biomass nutrient pools were 3.4–17 times greater in the plantations than in the control for all nutrient elements except Fe. With the exception of carbon and potassium, the soil nutrient pools were consistently higher in the mixed-species than in single-species treatments, and lowest in the control. These differences, as well as observed variations among plantation treatments, reflect differences in biomass productivity, nutrient content of plant tissues, and soil nutrient status at this age.

Nutrient concentrations varied greatly among biomass components for each of the three planted tree species as well as among species for each component (Table 4). Aboveground biomass (mass-weighted average) N was greatest in *Leucaena* (8.0–9.3 mg g^{-1}) than in *Casuarina* (4.6–5.6 mg g^{-1}) or *Eucalyptus* (4.1–4.8 mg g^{-1}). For phosphorus, these values were generally the highest in *Eucalyptus* (0.240–0.315 mg g^{-1}), intermediate in *Leucaena* (0.244–0.271 mg g^{-1}) and lowest in *Casuarina* (0.125–0.145 mg g^{-1}). Potassium concentrations in total aboveground biomass were higher in *Leucaena* (3.45–4.27 mg g^{-1}) than in *Eucalyptus* (2.14–2.78 mg g^{-1}) or *Casuarina* (1.71–2.09 mg g^{-1}). For Ca, Mg, Mn and Na, *Eucalyptus* had higher average concentrations of these elements in aboveground biomass than either of the N_2-fixing species.

Estimated total carbon stores ranged from 116 to 128 Mg ha^{-1} in the plantations and 83 Mg ha^{-1} in the control plots. At this age, soil carbon stores were ≈6–41% greater in the control than in the plantations. However, biomass and forest floor (litter) carbon stores, comprising 31–52% of the system total in the plantation (vs. 3.7% in the control), were 12.5–22.2 times greater in the plantations. Among plantation treatments, total carbon storage reflected biomass productivity, and was greater in stands with *Casuarina* (120–128 Mg ha^{-1}) than those with only *Eucalyptus* and/or *Leucaena* (116–117 Mg ha^{-1}).

Total nitrogen stores were 22–84% greater in the plantations (4003–6018 kg ha^{-1}) than in the control plots (3269 kg ha^{-1}). Increases in soil nitrogen ranged from 359 kg ha^{-1} (in the *Eucalyptus* monoculture) to 1779 kg ha^{-1} (in the *Casuarina*/*Leucaena* mixture) in the plantations relative to the control. Biomass N, comprising 7.8–19.1% of the system total in the plantations (vs. 1.7% in the control), ranged from 366 to 890 kg ha^{-1} among plantation treatments and was consistently greater in those containing *Leucaena* and lowest in the *Eucalyptus* monoculture.

Total phosphorus stores ranged from 39.0 to 63.6 kg ha^{-1} among plantation treatments (vs. 23.5 kg ha^{-1} in the control), and was greatest in treatments containing *Eucalyptus*. Biomass P comprised 34.6–45.8% of the total in the plantations, and 14.5% in the control. *Eucalyptus* had higher phosphorus concentrations in its woody biomass components than either *Casuarina* or *Leucaena*, and soils beneath these stands were also higher in available P.

Total potassium stores were also consistently greater in the plantation treatments (380–553 kg ha^{-1}) than in the control (224 kg ha^{-1}), with the highest values found in treatments with *Leucaena*. Biomass K comprised 48.1–64.5% of the total in the plantations (vs. 17.4% in the control). As with nitrogen, biomass K pools were greatest in plantation treatments containing *Leucaena* and least in the *Eucalyptus* monoculture, a reflection of tissue nutrient-concentration differences among the three plantation species. Soil K pools were reduced relative to the control in both, the *Eucalyptus* and *Leucaena* monocultures and the *Eucalyptus*/*Leucaena* mixture, and increased in the remaining treatments containing *Casuarina*.

Calcium, present in very large quantities in the soils at this site in the form of calcium carbonate, showed an increase in both, total and available soil stores in the plantations relative to the control. Compared with other nutrient elements, Ca stores in biomass were similar among plantation treatments (1002–1202 kg ha^{-1} vs. 152 kg ha^{-1} in the control), representing 12.5–16.7% of the system total. Soil Ca pools were highly variable, however, ranging from 5266 to

Table 6
Estimated nutrient stores in tree biomass, forest floor and soils (0–40 cm) in unplanted control plots and experimental plantations at 4 year[a]

	Unplanted control	*Casuarina equisetifolia*	*Eucalyptus robusta*	*Leucaena leucocephala*	*Casuarina + Eucalyptus*		*Casuarina + Leucaena*		*Eucalyptus + Leucaena*	
					Casuarina	*Eucalyptus*	*Casuarina*	*Leucaena*	*Eucalyptus*	*Leucaena*
Carbon (Mg/ha)										
aboveground biomass	1.4	48.2	29.3	32.4	31.6	12.3	40.7	15.3	14.1	31.4
roots	1.7	10.5	6.9	6.0	9.4		10.6		4.5	
litter (forest floor)	0.1	4.5	3.8	2.9	4.3		4.5		3.8	
soils (0–40 cm)	80.0	65.1	75.7	75.6	61.9		56.6		61.7	
Total	*83.2*	*128.3*	*115.7*	*116.9*	*119.5*		*127.7*		*115.5*	
Nitrogen (kg/ha)										
aboveground biomass	20	592	282	669	316	131	427	270	128	549
roots	33	108	84	227	104		193		87	
litter (forest floor)	1	131	63	115	79		134		77	
soils (0–40 cm)	3215	3863	3574	3678	4885		4994		4825	
Total	*3269*	*4694*	*4003*	*4689*	*5515*		*6018*		*5666*	
Phosphorus (kg/ha)										
aboveground biomass	1.4	15.3	19.7	17.5	9.3	8.1	11.3	8.4	7.5	18.7
roots	2.0	2.2	4.5	4.0	2.5		4.6		2.9	
litter (forest floor)	0.1	1.3	1.6	2.2	1.0		1.8		1.5	
soils (0–40 cm)	20.0	20.2	28.8	24.6	36.6		27.9		33.0	
Total	*23.5*	*39.0*	*54.6*	*48.3*	*57.5*		*54.0*		*63.6*	
Potassium (kg/ha)										
aboveground biomass	30	220	174	296	119	58	158	144	67	238
roots	9	25	27	49	23		51		27	
litter (forest floor)	1	8	8	9	7		11		10	
soils (0–40 cm)	185	202	171	160	209		189		173	
Total	*224*	*455*	*380*	*514*	*416*		*553*		*515*	
Calcium (kg/ha)										
aboveground biomass	18	838	998	901	521	358	589	367	402	69.7
roots	134	164	188	186	147		132		103	
litter (forest floor)	2	149	16.2	177	109		149		351	
soils (0–40 cm)	5157	6231	7787	5266	8424		6952		8083	
Total	*5311*	*7382*	*9135*	*6530*	*9559*		*8189*		*9636*	
Magnesium (kg/ha)										
aboveground biomass	5.0	66.4	102.6	96.8	41.8	55.3	53.9	44.4	55.0	89.5
roots	17.1	14.8	23.1	35.8	15.9		22.7		17.9	

litter (forest floor)	0.3	16.5	16.1	23.0		12.8			20.5			18.3	
soils (0–40 cm)	365.6	559.7	386.8	595.2		663.1			690.7			611.4	
Total	*388.6*	*657.4*	*528.6*	*750.8*		*788.9*			*832.2*			*792.1*	
Manganese (kg/ha)													
aboveground biomass	0.1	3.7	7.7	0.6	1.7		2.0	3.5		0.2	2.1		0.9
roots	1.2	0.7	1.0	1.4		0.6			0.6			0.7	
litter (forest floor)	0.0	1.4	1.6	1.0		1.0			1.4			0.9	
soils (0–40 cm)	38.3	52.7	50.0	46.3		86.2			65.8			73.3	
Total	*39.6*	*58.3*	*60.3*	*49.3*		*91.5*			*71.5*			*77.9*	
Sodium (kg/ha)													
aboveground biomass	2.5	49.1	35.2	10.4	45.7		29.9	33.8		5.6	30.8		22.2
roots	2.7	10.2	10.7	8.3		9.2			10.9			9.5	
litter (forest floor)	0.1	7.7	2.8	3.3		18.7			8.4			6.4	
soils (0–40 cm)	76.2	149.3	143.5	150.0		286.2			339.5			214.1	
Total	*81.5*	*216.3*	*192.2*	*172.0*		*389.7*			*398.2*			*283.0*	
Iron (kg/ha)													
aboveground biomass	1.0	11.5	4.2	4.9	4.2		2.1	5.2		1.8	6.7		9.5
roots	36.9	17.6	17.4	43.4		15.7			17.1			19.4	
litter (forest floor)	0.2	50.0	7.2	14.9		6.1			19.1			8.8	
soils (0–40 cm)	39.3	116.7	55.7	85.6		171.3			149.3			184.0	
Total	*77.4*	*195.8*	*84.5*	*148.8*		*199.4*			*192.5*			*228.4*	

[a] Tree biomass estimates based on measurements at 4.0 years and biomass nutrient data for trees harvested at 3.5 years; forest floor data based on sampling at 4.5 years; soil data (total C and N, available P and cations) from samples taken at 3.5 years.

8424 kg ha^{-1} among plantation treatments (vs. 5157 kg ha^{-1} in the control). Soil (available) Ca was highest in treatments containing *Eucalyptus*, and lowest in the *Leucaena* monoculture with no apparent correlation between these trends and biomass Ca concentrations among tree species.

Total magnesium stores were 36–114% greater in the plantations (529–832 kg ha^{-1}) than in the control plots (389 kg ha^{-1}), with the highest values in the mixed-species treatments and *Leucaena* monoculture. Biomass Mg pools ranged from 81.2 to 162.4 kg ha^{-1} (12.4–23.8% of the system total) among plantation treatments, as compared with 22.7 kg ha^{-1} (5.8% of total) in the control, and were greater in treatments comprised solely of *Eucalyptus* and/or *Leucaena* than in treatments with *Casuarina*. Soil Mg pools were lower in the control (366 kg ha^{-1}) and *Eucalyptus* monoculture (387 kg ha^{-1}) than in all other plantation treatments (560–691 kg ha^{-1}).

For the micronutrient elements Mn, Na, and Fe, total system stores, as well as biomass and soil pools, were generally much larger in the plantation treatments than in the control. Biomass pools for Mn and Na were markedly lower in *Leucaena* than in *Casuarina* or *Eucalyptus*.

Whole-tree (total aboveground biomass) harvest at four years would result in the removal of an estimated 25–44% of the total carbon stores and a significant proportion of the total nutrient capital from these plantation systems: 8–19% of total N; 35–46% of total P; 48–65% of total K; 13–17% of total Ca; 12–24% of total Mg; 1.2–13% of total Mn; 6–23% of total Na; and 3.2–7.1% of total Fe. As indicated in Fig. 7, the estimated 'nutrient costs' of harvestable (aboveground) biomass, expressed as kg nutrient element per Mg of biomass (dry weight), vary considerably among treatments. This variation is due to differences among species in biomass component nutrient concentrations (Table 4). Biomass nutrient costs in the mixed-species treatments were, almost without exception, intermediate between those of the monoculture treatments of their two component species.

For nitrogen, whole-tree harvest nutrient costs in the single-species treatments were lowest for *Eucalyptus* (4.51 (kg N) Mg^{-1} biomass), intermediate for *Casuarina* (5.62 (kg N)/Mg biomass), and highest for *Leucaena* (9.32 (kg N)/Mg biomass). These values for phosphorus followed a somewhat different trend and were lowest for *Casuarina* (0.145 (kg P)/Mg biomass), intermediate for *Leucaena* (0.244 (kg P)/Mg biomass), and highest for *Eucalyptus* (0.315 (kg P)/Mg biomass). In the case of potassium, *Casuarina* had the lowest whole-tree biomass nutrient costs (2.09 (kg K)/Mg biomass), *Leucaena* the highest (4.13 (kg K)/Mg biomass), with an intermediate value for *Eucalyptus* (2.79 (kg K)/Mg biomass). Whole-tree nutrient costs for calcium and magnesium followed trends similar to those for phosphorus. These were lowest for *Casuarina* (8.0 kg Ca and 0.63 kg Mn per Mg biomass), intermediate for *Leucaena* (12.6 kg Ca and 1.35 kg Mn per Mg biomass), and highest for *Eucalyptus* (16.0 kg Ca and 1.64 kg Mn per Mg biomass).

Despite significant nutrient exports from the site that would be associated with whole-tree harvests, these projected losses would generally be more than compensated for carbon and nutrient accretion in plantation soils, roots and litter during the four years of tree growth at this site. Only for carbon and potassium would whole-tree harvests exports result in a net loss of these elements in certain treatments relative to unplanted (control) areas. In the case of carbon, the net system losses are estimated to be 3.7% in the *Casuarina* monoculture, 9.1% in the *Casuarina*/*Eucalyptus* mixture, 13.8% in the *Casuarina*/*Leucaena* mixture and 15.9% in the *Eucalyptus*/*Leucaena* mixture, or 3.1–13.2 Mg ha^{-1} in these treatments. For potassium, net system losses are estimated to range from 6.0 to 19.7 kg ha^{-1}, or 2.7% in the *Leucaena* monoculture, 6.3% in the *Eucalyptus*/*Leucaena* mixture, and 8.0% in the *Eucalyptus* monoculture.

To reduce harvest-related nutrient exports, a more conservative approach involving removal of only larger diameter (>2.5 cm) stems and branches might be recommended to retain more of the accumulated nutrient capital on-site (Fig. 7). Relative to whole-tree harvests, this harvest option would reduce biomass nutrient costs by 13–36% for nitrogen, 13–39% for phosphorus, and 17–30% for potassium. For calcium, this harvest option would result in either a very small (4–11%) reduction in biomass nutrient costs or a small increase (+5.1%) in the case of *Eucalyptus* monoculture. Similarly, nutrient costs for magnesium biomass would be increased slightly (+3.7%) in the *Eucalyptus* monoculture, though reduced from 16% to 83% among the other plantation treatments.

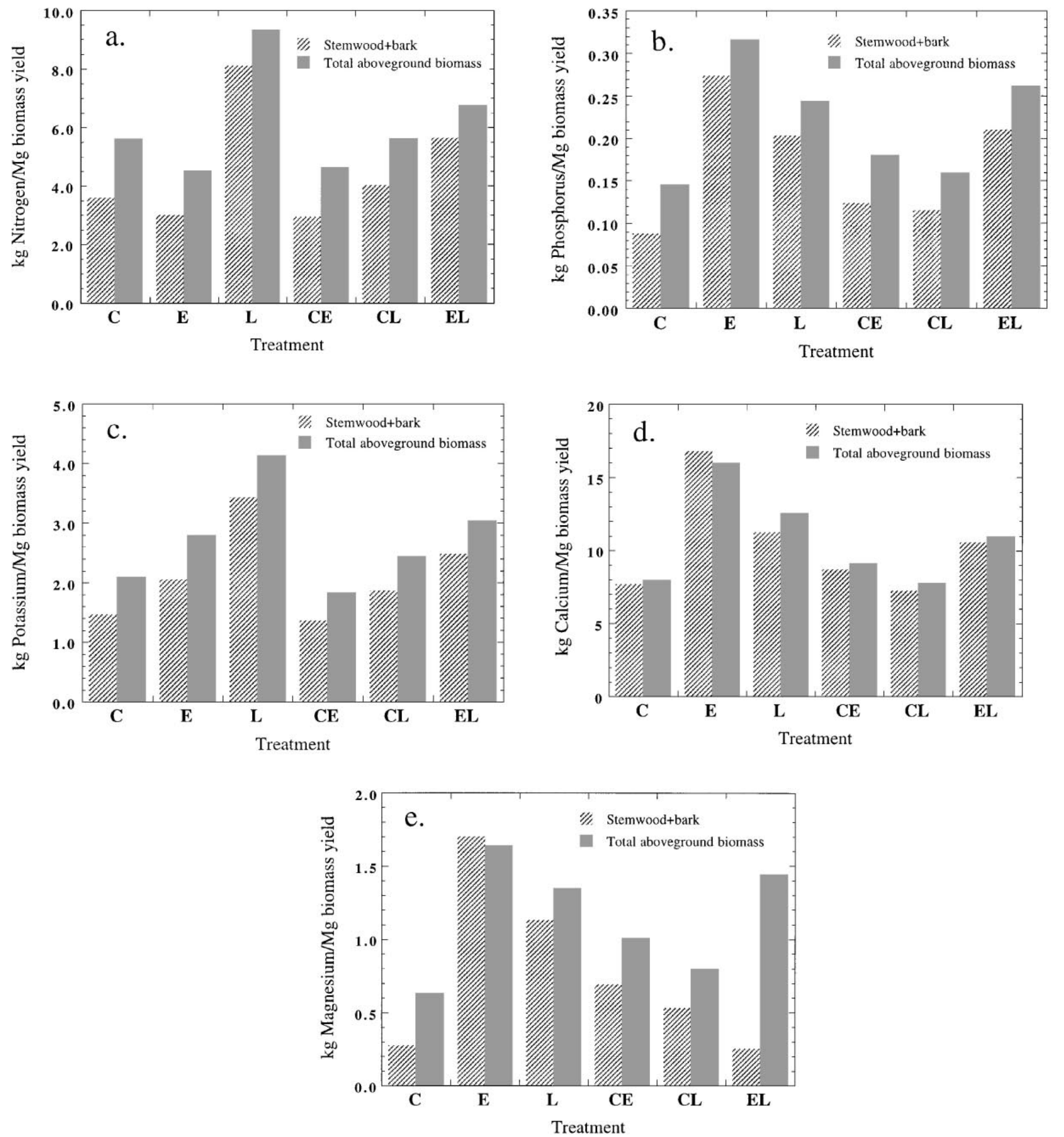

Fig. 7. Estimated nutrient content per ton biomass yield for whole-tree (total aboveground) vs. stemwood+ bark (including branches <2.5 cm diameter) harvest options in four-year-old single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala*. (a) Nitrogen; (b) Phosphorus; (c) Potassium; (d) Calcium; and (e) Magnesium.

3.5. Understory forest regeneration

At 8.5 years after plantation establishment, a total of 24 tree and shrub species were recorded in the plantation understories (Tables 7 and 8). Of these, only one (*Albizia lebbek*) was found in the unplanted control plots. With the exception of *Acacia auriculiformis* and *Albizia lebbek*, which originated from trees planted

Table 7
Tree and shrub species colonizing study plantation understories (all treatments) at 8.5 year Importance values calculated as sum of relative density and relative frequency among all plantation treatment plots.

Species	Family type	Fruit type	Principal dispersal agent	Density (No m^{-2})	Frequency	Importance value
Calophyllum brasiliense	Hypericaceae	large drupe	bats	0.855	0.88	70.7
Schinus terebinthifolius	Anacardiaceae	fleshy drupe	birds	0.250	0.82	27.4
Citharexylum fruticosum	Verbenaceae	fleshy drupe	birds	0.108	0.88	18.0
Cordia polycephala	Boraginaceae	fleshy drupe	birds	0.066	0.76	13.7
Andira inermis	Leg.-Papilionoideae	large drupe	bats	0.042	0.76	11.9
Bourreria succulenta	Boraginaceae	fleshy drupe	birds	0.017	0.82	10.9
Acacia auriculiformis	Leg.-Mimosoideae	dehiscent pod	wind	0.024	0.59	8.6
Bursera simaruba	Burseraceae	drupelike capsule	birds	0.012	0.47	6.4
Terminalia catappa	Combretaceae	large drupe	bats	0.005	0.35	4.5
Murraya paniculata	Rutaceae	fleshy drupe	birds	0.003	0.29	3.7
Spathodea campanulata	Bignoniaceae	dehiscent capsule	wind	0.006	0.24	3.2
Ixora coccinea	Rubiaceae	fleshy berry	birds	0.003	0.24	3.0
Roystonea borinquena	Palmae	slightly fleshy berry	birds	0.003	0.24	3.0
Psidium guajava	Myrtaceae	fleshy berry	birds	0.003	0.24	3.0
Rauvolfia nitida	Apocynaceae	fleshy drupe	birds	0.002	0.18	2.2
Coccoloba diversifolia	Polygonaceae	fleshy berry	birds	0.004	0.12	1.7
Zanthoxylum marinicense	Rutaceae	dehiscent capsules	birds	0.002	0.12	1.5
Albizia lebbek	Leg.-Mimosoideae	dehiscent pod	wind	0.001	0.12	1.5
Cordia nitida	Boraginaceae	fleshy drupe	birds	0.001	0.12	1.5
Sideroxyllum salicifolia	Sapotaceae	fleshy berry	birds	0.002	0.06	0.9
Casearia guianensis	Flacourtiaceae	dehiscent capsule	birds	0.001	0.06	0.7
Clusia rosea	Clusiaceae	fleshy capsules	bats	0.001	0.06	0.7
Lonchocarpus latifolius	Leg.-Papilionoideae	dehiscent pod	wind	0.001	0.06	0.7
Melicoccus bijugata	Sapindaceae	slightly fleshy drupes	bats	0.001	0.06	0.7
			Total	1.413		200.0

nearby at the experiment site, these species are typically found in local secondary forests or are planted in gardens or along roads within a kilometer of the plantations. The majority of these produce seeds that are dispersed by birds although several, including the most common species, *Calophyllum brasiliense*, produce larger seeded fruits that are transported and consumed by bats.

The density of trees and shrubs regenerating beneath the plantations increased steadily during the study period, averaging 0–0.16 individuals m^{-2} among treatments at 2.5 years, 0.03–0.31 individuals m^{-2} at 4.5 years and 0.77–2.90 individuals m^{-2} at 8.5 years (Fig. 8). The majority of these understory colonists were seedlings or saplings <2 m tall; these comprised between 89.7% and 99.7% of the total regeneration density among treatments at 8.5 years. The density of larger individuals ($\geq$2 m tall) ranged from 0.003 individuals m^{-2} in the *Casuarina*/*Leucaena* treatment to 0.083 individuals m^{-2} in both the *Leucaena* monoculture and *Casuarina*/*Leucaena* mixed-species stands, with no significant differences among plantation treatments. Understory regeneration density at 8.5 years was significantly greater in the *Casuarina* monoculture than in either the *Eucalyptus* monoculture or the *Eucalyptus*/*Leucaena* mixed stands ($p < .05$, Fisher's PLSD).

Understory tree and shrub species richness at 8.5 years ranged from 6.3 species/plot in the *Casuarina* monocultures to 11.0 species/plot in the mixed *Eucalyptus*/*Leucaena* stands; treatment means were significantly different only between these two treatments for individuals <2 m tall ($p < .05$, Fisher's PLSD). Species richness of larger individuals ($\geq$2 m tall) was only 4–35% of that for those in the smaller (<2 m) size class and ranged from 0.3 species per plot in the *Casuarina*/*Leucaena* treatment to 3.3 species per plot in the *Leucaena* treatment; treatment differences were not significant.

Table 8
Litter accumulation and characteristics of understory regeneration for colonizing secondary forest tree and shrub species in plantation and grassland control plots at 8.5 year[a]

	Unplanted control	*Casuarina equisetifolia*	*Eucalyptus robusta*	*Leucaena leucocephala*	*Casuarina* + *Eucalyptus*	*Casuarina* + *Leucaena*	*Eucalyptus* + *Leucaena*	ANOVA[c]
Mean litter depth (cm)[b]	2.0bc	3.4a	1.8bc	0.9c	3.3ab	3.4a	1.6bc	*
Regeneration density (No. m^{-2}):								
all stems	0.01b	2.90a	0.81b	2.02ab	1.95ab	1.59ab	0.77b	ns
stems <2 m tall	0.01b	2.89a	0.78b	1.94ab	1.94ab	1.59ab	0.69b	ns
stems $\geq$2 m tall	0a	0.009a	0.020a	0.083a	0.005a	0.003a	0.083a	ns
Tree species richness (No./plot):								
all stems	0.5c	6.3b	9.0ab	9.3ab	7.0ab	7.7ab	11.0a	*
stems <2 m tall	0.5c	6.3b	8.7ab	9.3ab	6.5ab	7.7ab	11.0a	*
stems $\geq$2 m tall	0b	1.0ab	0.7ab	3.3a	0.5ab	0.3ab	2.7ab	ns
Species diversity (H'):								
all stems	0d	0.13cd	0.60ab	0.60ab	0.22cd	0.38bc	0.81a	***
stems <2 m tall	0d	0.12cd	0.56ab	0.56ab	0.21cd	0.38bc	0.76a	***
stems $\geq$2 m tall	0a	0.007a	0.05a	0.11a	0.009a	0.004a	0.009a	ns

[a] $n = 3$ replicate 100 m^2 plots per treatment, except for unplanted control and *Casuarina* + *Eucalyptus* treatments ($n = 2$).
[b] Mean of average litter depths measured at 10 points in each 100 m^2 sub-plot for each treatment; $n = 3$ plots per treatment.
[c] ANOVA results: ns, treatment effect not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. Similar letters within a row indicate treatment means that were similar ($p < 0.05$, Fisher's PLSD).

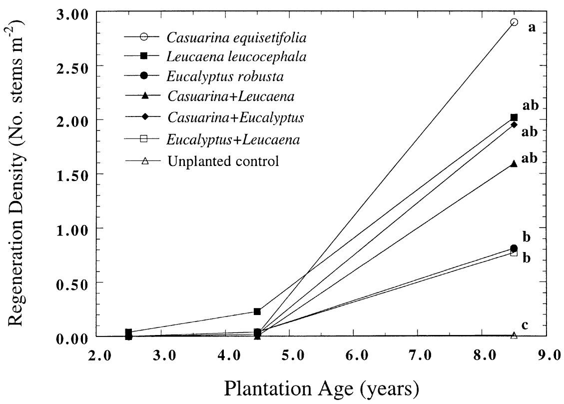

Fig. 8. Understory regeneration density for secondary forest trees and shrubs in experimental plantations to 8.5 years. Similar letters to right of curves indicate that mean densities at 8.5 years were not significantly different among treatments ($p < .05$, Fisher PLSD).

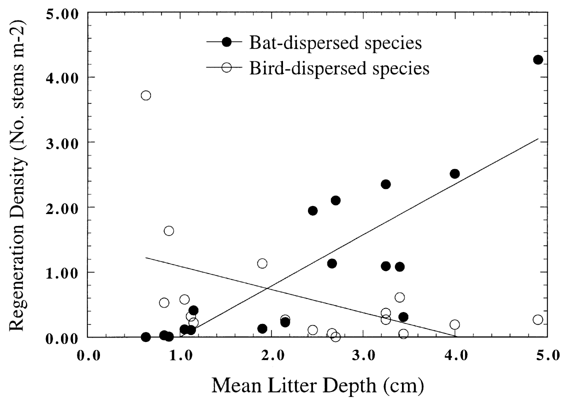

Fig. 9. Relation between understory seedling density for secondary forest trees and shrubs and litter depth. For bat-dispersed species: $y = -0.79 + 0.78x$ ($r^2 = 0.67$; F = 30.48; $p < .0001$). For bird-dispersed species: $y = 1.44 - 0.36x$ ($r^2 = 0.25$; F = 5.01; $p < .05$).

Tree species diversity (Shannon–Wiener: H') was significantly greater in the *Eucalyptus*/*Leucaena* mixed species plots (mean: 0.76) than in all treatments that included *Casuarina* (range of means: 0.12–0.38); both the *Eucalyptus* and *Leucaena* monocultures had significantly higher mean H' values than either the *Casuarina* or *Casuarina*/*Eucalyptus* treatments ($p < .001$; Fisher's PLSD). Species diversity for trees >2 m in height was low for all treatments (range of H' means: 0.004–0.11) with no significant differences among treatments.

These data reveal several general trends among plantation treatments with regard to understory regeneration density and species diversity. Treatments containing *Casuarina* (in particular, the *Casuarina* monoculture) tended to have a greater understory regeneration density but a lower species richness and diversity than treatments comprising *Eucalyptus* and/or *Leucaena*. Differences in regeneration density among treatments were due, in large part, to the presence or absence of the most common understory species, *Calophyllum brasiliense*, which was more abundant in treatments that included *Casuarina* (range of means: 1.17–2.83 individuals m^{-2}) than in treatments including only *Eucalyptus* and/or *Leucaena* (range of means: 0.04–0.50 individuals m^{-2}). Differences among treatments in litter accumulation appear to have a role in explaining both, the relative abundance of this species and overall patterns of regeneration density and diversity. Litter depths at 8.5 years were significantly greater in plots with *Casuarina* (range of treatment means: 3.3–3.4 cm) than in those without *Casuarina* (range of treatment means: 0.9–1.8 cm). As shown in Fig. 9, there was a significant positive relationship between litter depth and regeneration density for the bat–dispersed species (including *Calophyllum brasiliense*) and a significant inverse relationship between litter depth and regeneration density for the more numerous secondary forest species with bird-dispersed seeds. It appears that the deeper litter layer that characterizes stands with *Casuarina* may act as a barrier to germination and establishment of tree species with smaller, bird-dispersed seeds that comprise the majority of tree species occurring beneath the plantations. The typically bat-dispersed species such as *C. brasiense*, *Andira inermis*, and *Terminalia catappa*, have large seeds with sufficient reserves for their roots to penetrate the thick litter layer beneath *Casuarina*. Alternatively, there may be differences in perch selection behavior between the birds and bats that are the primary seed dispersers at this site that are responsible for the observed differences in understory regeneration among treatments. Data on seed rain and wildlife observations would be required to sort out these alternative or additive causal relationships.

4. Discussion

Tree growth rates and biomass development for *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leu-*

caena leucocephala in this study were within the range of values reported for these species in other tropical locations (National Research Council, 1983, 1984a; National Research Council, 1984b, b; Parrotta, 1992a; MacDicken, 1994). While the biomass productivity of *Eucalyptus* was clearly unaffected by admixture with either N_2-fixing species at four years, biomass production in both *Casuarina* and *Leucaena* was clearly greater in the mixed-species treatments. Relative to the single-species treatments, *Casuarina* aboveground biomass yields increased in mixed stands with both, *Eucalyptus* (+33%) and *Leucaena* (+72%). *Leucaena* aboveground biomass yields were unaffected when grown with *Casuarina* (+6%) but increased in admixture with *Eucalyptus* (+92%).

The increase in total biomass productivity in the mixed-species treatments relative to the single-species stands is consistent with the results of studies in Hawaii, in which total biomass productivity at six years was greater in 50 : 50 mixtures of *Eucalyptus saligna* or *E. grandis* with either *Albizia* [*Paraserianthes*] *falcataria* or *Acacia melanoxylon* than in single-species stands of these species (DeBell et al., 1985; Binkley et al., 1992; DeBell et al., 1997). In the Hawaiian studies, the productivity advantage of mixtures accrued to *Eucalyptus*, in contrast to the present study in which admixture with either N_2-fixing species had little or no effect on *Eucalyptus* growth and biomass production. The enhanced aboveground productivity of the mixed *Eucalyptus–Albizia* plantations in Hawaii was attributed to their increased light interception and light-use efficiency, and to increased nutrient availability and nutrient-use efficiency by *Eucalyptus* relative to pure *Eucalyptus* stands (Binkley et al., 1992).

The lack of growth response by *Eucalyptus* to admixture with either N_2-fixing tree species is perhaps surprising, considering the high estimated rates of nitrogen fixation by *Leucaena* and *Casuarina* in the mixed-species stands with *Eucalyptus* (73–74 kg N ha^{-1} $year^{-1}$; Parrotta et al., 1996) and higher rates of nutrient cycling in these stands relative to the *Eucalyptus* monoculture. Nitrogen concentrations in fresh leaves or total aboveground biomass, and N retranslocation prior to leaf-fall, were not significantly different among treatments for *Eucalyptus*, which suggests that association with either N_2-fixing species is not (yet?) having any positive influence on nutrient availability for *Eucalyptus*.

The increased productivity of both *Casuarina* and *Leucaena* in the mixed-species stands in the present study is not easily explained and may be due to several factors. As the data presented in Table 5 show, soils beneath the mixed-species plantation treatments tended to have higher initial (0.2 year) levels of soil organic matter, total nitrogen, and available magnesium, but lower levels of available phosphorus and available potassium than those in the single-species *Leucaena* and *Casuarina* treatments. It is not clear whether or not these initial differences, particularly for soil nitrogen, could account for the observed differences in their growth and yield. In the case of *Casuarina*, biomass nitrogen and phosphorus concentrations were generally higher and retranslocation lower in the single-species stands than in mixed-species stands with *Eucalyptus* or, particularly, with *Leucaena*. These results suggest that nutrient-use efficiency in *Casuarina* was greatest in the mixed stands with *Leucaena*, intermediate in mixture with *Eucalyptus*, and lowest in the monoculture. For *Leucaena*, however, treatment differences in biomass nutrient concentrations and retranslocation did not show any clear trends although foliar, whole-tree, and litter nitrogen concentrations were lower in the single-species than in either of the mixed-species treatments. Possible differences in light-use efficiency between trees grown in single- and mixed-species stands might also explain the observed treatment differences in biomass productivity of *Leucaena* and *Casuarina* (Binkley et al., 1992).

Other studies comparing single- and mixed-species plantations in the tropics have failed to show any consistent productivity advantages of mixed-species over monospecific plantings (FAO, 1992; Montagnini et al., 1995). In a study comparing single- and mixed-species stands of *Eucalyptus urophylla* and *Leucaena leucocephala* in Espirito Santo, Brazil (Moraes de Jesus and Brouard, 1989), total wood volume at seven years was greatest in the pure *Eucalyptus* stands, intermediate in the mixtures and lowest in the pure *Leucaena* stands; *Eucalyptus* mortality was higher in the mixed stands, as it was in the present study.

Litterfall production and rates of nutrient return, highest in *Leucaena*, lowest in *Eucalyptus* and intermediate in *Casuarina* and mixed-species stands for most elements, generally followed expected trends.

Several studies comparing *Leucaena* or other legume trees (such as *Acacia* and *Albizia* spp.) with *Eucalyptus* spp. have reported similar trends, i.e. higher litterfall productivity, higher rates of nutrient return (particularly for N and P), and more rapid litter decomposition under these N_2-fixing species, than under *Eucalyptus* (Gill et al., 1987; Bhardwaj et al., 1992; Binkley, 1992; Binkley et al., 1992, 1997; Toky and Singh, 1993, 1995; Binkley and Giardina, 1997).

Patterns of nutrient storage in aboveground biomass in this study were also broadly similar to those reported for these and related species at other tropical locations (da Silva et al., 1983; Parrotta, 1989; Wang et al., 1991; Toky and Singh, 1995; Binkley et al., 1997). Among species, aboveground biomass N and K concentrations were greatest for *Leucaena*, while P, Ca, and Mg concentrations were greatest for *Eucalyptus*; the lowest aboveground biomass nutrient element concentrations were found in *Casuarina*. As a result, the estimated nutrient costs of whole-tree harvest differed among species and, depending on the element, were usually lower for *Casuarina* than for either *Eucalyptus* or *Leucaena*, a very similar trend to that reported by Wang et al. (1991) who studied these same species under very different site conditions elsewhere in Puerto Rico.

Plantation effects on soils in this study were inconclusive, but suggest several general trends over the 7.5-year study period. These apparent trends and treatment differences should be viewed with some caution, however, due to the high initial soil variability among treatments replicates and the somewhat higher average organic matter, total N and available P and cation content in the mixed-species treatments at the start of the experiment (Table 5).

Relative to the control treatment, soil pH increased in stands comprised or *Casuarina* and/or *Leucaena* and declined in the three remaining treatments that included *Eucalyptus*. This contrasts with the findings of most studies, which report slight-to-moderate pH decreases in soils beneath tropical plantation species, including N_2-fixing legumes, *Casuarina equisetifolia*, and eucalypts (Herbert, 1984; Sánchez et al., 1985; Maily and Margolis, 1992; Sankaran et al., 1993; Rhoades and Binkley, 1996). Organic-matter content and effective cation exchange capacity decreased in all plantation soils relative to the control. These decreases in soil organic matter beneath plantations may be due to increased biological activity (decomposition) in plantations.

Total N and available P increased in the unplanted control as well as in most plantation treatments with the exception of the single-species stands of *Casuarina* and, particularly, of *Eucalyptus*, which declined over this period. Available K increased in all treatments (124-203 kg ha^{-1}; 0–20 cm depth), with higher gains in the mixed-species than in single-species or control treatments. Available Ca declined sharply in all plantation treatments but increased slightly in the control treatment. Increases in soil N in plantations containing N_2-fixing species, particularly leguminous trees, are commonly reported in the literature (Sánchez et al., 1985; DeBell et al., 1989; Toky and Singh, 1995; Binkley, 1997), as are decreases in soils beneath *Eucalyptus* (Bargali et al., 1993) and *Casuarina* (Maily and Margolis, 1992). Wang et al. (1991) found significantly higher N concentrations in the surface (0–3 cm) soils in 5.5-year-old plantations of *Leucaena leucocephala* than in those of *Casuarina equisetifolia* which, in turn, had higher soil N concentrations than those beneath *Eucalyptus robusta*. Similarly, DeBell et al. (1989) reported increases in soil N beneath four-year-old stands of *Albizia falcataria* and mixed *Albizia/Eucalyptus* stands than in pure *Eucalyptus* stands in Hawaii. With respect to soil P and exchangeable cations, there are no consistent trends in the literature regarding the differential effects of *Leucaena*, *Casuarina* and *Eucalyptus*; these effects appear to be highly site-specific and dependent on initial soil conditions.

All plantation treatments included in this study provided a favorable environment for the recruitment and regeneration of a variety of native secondary-forest tree and shrub species, in contrast to the unplanted control plots in which only a single tree species was found to have regenerated naturally at very low densities. There were no significant differences in understory regeneration patterns between single- and mixed-species plantations. Rather, differences in the understory regeneration density and species diversity among treatments were due primarily to the presence or absence of *Casuarina*; in the three treatments that included *Casuarina*, understory regeneration was dominated by a large-seeded, bat-dispersed species (*Calophylum brasiliense*) with a fewer number of other tree species than treatments whose overstories were comprised of only *Leucaena* or *Eucalyptus*. Earlier analyses of understory development in these plantations at 4.5 year showed similar species-richness trends, but greater regeneration density beneath *Leucaena* than either *Eucalyptus* or *Casuarina* (Parrotta, 1995). The temporal patterns of understory regeneration in all stands closely followed those in plantations of *Albizia lebbek* at this site (Parrotta, 1992b), with both species richness and abundance increasing steadily from Age 2 onward.

These results show that all three species, whether native (*Leucaena*), naturalized exotic (*Casuarina*) or exotic (*Eucalyptus*), are capable of catalyzing native forest succession on this deforested, degraded site where natural regeneration processes in the absence of planted tree cover are seriously impeded by the absence of a viable soil seed bank, limitations on seed inputs by wildlife, grass competition, and unfavorable microenvironmental conditions (Parrotta, 1992b, 1995; Lugo, 1997; Parrotta et al., 1997). Thus, for the purposes of forest rehabilitation and restoration on degraded tropical lands, such plantations under appropriate management can serve a dual role by accelerating natural recovery of species-rich forest ecosystems while providing needed wood products to populations faced with shortages of fuelwood, timber and other forest products (Parrotta and Turnbull, 1997).

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