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Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site

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Abstract. Patterns of understory colonization by native and naturalized trees and shrubs were evaluated in 4.5-year-old plantations of three exotic tree species, *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala,* on a degraded coastal grassland site with reference to overstory composition and understory environmental conditions. 19 secondary forest species were established in the plantation understories (with a total area of 0.52 ha), while no natural regeneration occurred in unplanted, though protected, control areas. The majority of these species (90 %) and the total seedling population (97 %) were zoochorous, indicating the importance of frugivorous bats and particularly birds as facilitators of secondary forest species colonization. Understory species richness and seedling densities were affected significantly by overstory composition, the most abundant regeneration occurring beneath *Leucaena* and least under *Casuarina*. Understory colonization rates within mixed-species stands were intermediate between those of single-species stands of the trees comprising their overstories. Significant negative correlations were found between understory species richness and seedling density, and forest floor depth and dry mass, especially for small-seeded ornithochorous species. Higher colonization rates near the peripheries of plantation plots relative to plot interiors were due in part to roosting site preferences by frugivores, particularly bats.

The study results indicate that overstory species selection can exert a significant influence on subsequent patterns of colonization by secondary forest species and is an important consideration in the design of plantations for 'catalyzing' succession on deforested, degraded sites.

Keywords: Biodiversity; *Casuarina equisetifolia*; *Eucalyptus robusta*; *Leucaena leucocephala*; Natural regeneration; Puerto Rico; Restoration ecology; Succession.

Nomenclature: Liogier (1982).

Introduction

In tropical and subtropical regions where extensive degradation of forests, rangelands, and agricultural lands often has severe social and economic implications, reforestation programs designed and managed to satisfy local needs for a diverse forest product mix are likely to assume an increasingly important role in the future (Brown & Lugo 1994). To date, tropical forestry research has made significant contributions towards the rehabilitation of degraded tropical landscapes through the identification of stress-tolerant native and exotic tree species and design of management systems for maximizing plantation productivity under a wide range of degraded site conditions. Research on the effects of various plantation species and management options on soil improvement and nutrient cycling processes, conducted during the past 20 years, is likely to contribute significantly to the development of sustainable silvicultural systems for degraded tropical lands.

Given the high degree of dependence on a wide range of wood and non-wood forest products in many tropical countries, the traditional focus of 'wasteland' reforestation programmes on maximizing productivity of the planted crop (for fuelwood and/or timber) may need to be broadened if 'rehabilitation forestry' is to gain public support and thus yield significant environmental and socio-economic benefits. Recent experiences in India and Southeast Asia have demonstrated that community-based reforestation projects aimed at the rehabilitation of species-rich secondary forests on degraded lands can yield excellent results when traditional forestry practices are adapted to facilitate regeneration of locally valued native species (Anon. 1993; Poffenberger and McGean 1994).

Recent studies in Puerto Rico (Lugo 1988, 1992; Parrotta 1992, 1993a; Lugo et al. 1993) and China (Brown & Lugo 1994) have shown that forest plantations established on degraded sites long devoid of native forest cover can act as 'successional catalysts', facilitating recolonization of native flora through their influence on understory microclimate and soil fertility, suppression of dominant grasses, and provision of habitat for seed-dispersing wildlife. This 'catalytic' effect appears to be a widespread phenomenon, supported by observations and understory floristic data from plantations established under a variety of degraded site conditions, including mined lands, in India (Mathur et al. 1980;

Mathur & Soni 1983; Prasad & Pandey 1985; Soni et al. 1989; Bajaj 1990), Malaysia (Mitra & Sheldon 1993), Papua New Guinea (D. Lamb 1994, pers. comm.), Congo (H. de Foresta 1994, pers. comm.), and Brazil (Good et al. 1993; Parrotta 1994 pers. obs.).

A number of factors affecting the rate of plantation understory colonization by native (or naturalized) tree and shrub species are suggested by these and other successional studies in plantations, abandoned pastures, and mined lands in both tropical and temperate regions. These factors relate to initial site conditions as well as plantation design and management practices. The former include: the degree of site degradation, particularly the availability of rootstocks and seed banks (Mathur & Soni 1983; Chaubey et al. 1988a, b; Prasad & Pandey 1989); landscape floristics and proximity to native forest stands, i.e., seed sources (Peterken & Game 1984; McClanahan 1986; Hardt & Forman 1989; van Ruremonde & Kalkhoven 1991; Dzwonko & Loster 1992; Parrotta 1993a; Dzwonko 1993); and presence of seed-dispersing wildlife populations (Guevara et al. 1986, 1992; McClanahan & Wolfe 1993; Mitra & Shelton 1993). The latter include: tree spacing (A. Chiarucci 1994, pers. comm.); plantation age (Bhaskar & Dasappa 1986; Chaubey et al. 1988b; Lugo et al. 1993; Parrotta 1993a), understory management intensity and degree of protection from fire and other site disturbances (Bajaj 1990; Brown & Lugo 1994); and plantation species selection, or overstory composition (Srivastava 1986; Pande et al. 1988; Lugo 1988, 1992).

The choice of species may affect understory colonization in several ways as tree species will differ in their 'attractiveness' as roosting habitat for seed-dispersing birds and bats (Debussche et al. 1982; Manders & Richardson 1992; Mitra & Sheldon 1993); canopy architecture and influence on understory light, temperature and humidity regimes (Richardson et al. 1989; Parrotta 1993a); rates of leaf litter production, decomposition, and litter chemistry (Suresh & Vinaya Rai 1988); and influence on soil biological activity and other aspects of soil fertility.

At present, our understanding of how these factors influence succession within plantation ecosystems is very limited. Systematic studies are required to understand their relative importance and implications for plantation design and management so as to realize the potential of these systems as successional catalysts.

In this paper, the influence of overstory species composition on patterns of woody tree and shrub species colonization is evaluated in young, single- and mixed-species plantations of *Casuarina equisetifolia*, *Leucaena leucocephala* and *Eucalyptus robusta* on a severely degraded coastal site in Puerto Rico. These exotic species were chosen for study because of their contrasting growth forms and ecological characteristics, and their extensive use in rehabilitation and short rotation plantation programs in the tropics.

Material and Methods

Study area

The study area is located at the University of Puerto Rico's Toa Baja experimental station located on the northern (Atlantic) coast of Puerto Rico (18° 27' N, 66° 10' W). Annual precipitation averages 160 cm and is moderately seasonal in distribution. Average daily temperatures range from 23.8 °C in January to 29.4 °C in August. The soils are well-drained, alkaline, calcareous sands.

Formerly supporting coastal dune forest vegetation, the site has been subject to frequent and often severe disturbances during the past century, including forest clearing, cattle grazing, cultivation, topsoil removal, and periodic fires. Presently the surrounding landscape is dominated by residential housing or commercial and industrial facilities, with secondary forest vegetation restricted to roadsides and a 10-ha abandoned pasture, adjacent to the southern edge of the study site, supporting ca. 20 native and naturalized tree species.

At the time of experimental plantation establishment, the study site was dominated by grasses, principally *Panicum maximum* and *Tricholaena repens*, with ca. 30 species of herbs and vines, principally *Asteraceae*, *Papilionaceae* and *Euphorbiaceae*; woody plants were absent (Parrotta 1993b).

Experimental plantations were established in 1989 using a randomized block design with three replicate 16 m × 16 m plots of each of the following treatments:
(1) *Casuarina equisetifolia* monoculture (CM);
(2) *Eucalyptus robusta* monoculture (EM);
(3) *Leucaena leucocephala* monoculture (LM);
(4) *Eucalyptus* + *Casuarina* (EC);
(5) *Casuarina* + *Leucaena* (CL);
(6) *Eucalyptus* + *Leucaena* (EL); and
(7) unplanted control.

These plantations were established as part of a larger study to evaluate biomass productivity, nutrient cycling, and biological nitrogen fixation in single- and mixed-species stands (Parrotta et al. 1994a, b). The initial tree spacing in all forest plots was 1 m × 1 m; in the two-species treatments (1:1 mixtures), seedlings were planted in a checkerboard pattern. Plantation plots were separated from one another by buffer strips (unplanted alleys) 5 m in width, and the unplanted control plots were located outside of the main block of 18 forest plots.

The plantations were neither irrigated nor did they

Table 1. Characteristics of the plantations[1]. Values following means indicate standard errors; n = 3 replicates per treatment.

	Treatment[2]					
	LM	CM	EM	EL	EC	CL
Average tree density (stems/ha)	9500	7100	4800	6350	4400	8300
Average stem diameter (cm)	7.0	7.7	10.0	7.7	10.2	7.1
Average tree height (m)	8.4	9.7	9.4	9.8	11.6	9.6
Above-ground biomass (kg/m^2)	7.2 ± 1.8	10.5 ± 0.4	6.3 ± 0.2	10.0 ± 2.3	9.7 ± 1.4	12.4 ± 1.2
Fine root mass (kg/m^2)	0.25 ± 0.12	0.19 ± 0.10	0.32 ± 0.08	0.17 ± 0.08	0.19 ± 0.02	0.20 ± 0.11
Forest floor mass (kg/m^2)	0.73 ± 0.07	1.05 ± 0.10	0.90 ± 0.03	0.88 ± 0.08	0.99 ± 0.03	1.08 ± 0.05
Forest floor depth (cm)	1.3 ± 0.2	2.5 ± 0.2	1.5 ± 0.2	1.5 ± 0.2	2.1 ± 0.5	2.4 ± 0.1
Leaf area index (2.5-4.5 yr)	2.2 ± 0.2	3.1 ± 0.1	2.6 ± 0.1	2.1 ± 0.1	2.5 ± 0.1	2.7 ± 0.1
Soil organic matter (%)	6.0 ± 1.4	5.5 ± 1.0	4.6 ± 0.5	7.3 ± 1.4	8.3 ± 1.2	5.6 ± 0.6

[1] Plantation age = 4 yr for tree density, stem diameter, tree height, above-ground and fine root biomass; 4.5 yr for forest floor mass and depth; 3 yr for soil organic matter.
[2] Treatments: LM = *Leucaena leucocephala*, CM = *Casuarina equisetifolia*, EM = *Eucalyptus robusta*, EL = *Eucalyptus* + *Leucaena*, EC = *Eucalyptus* + *Casuarina*, CL = *Casuarina* + *Leucaena*.

receive fertilizer amendments. During the first 6 months after planting, the forest plots were manually hoed to control weed competition. Thereafter all planted and control plots were protected from understory disturbances, particularly grazing and fire.

Data collection and analysis

The floristic composition of plantation understory and control plots was monitored 1.0, 2.5, and 4.5 yr after plantation establishment. For these surveys each plantation plot was divided into two zones: (1) a central 11 m × 11 m central subplot, and (2) a 168 m^2 buffer, or edge zone, that included the three peripheral tree rows. Species richness and percentage cover (6-point cover scale) were recorded for grasses, forbs, vines, and woody species in all plots. For tree and shrub species, all seedlings and saplings were counted and their heights recorded.

Tree and shrub species encountered in these surveys were classified with respect to their dispersal characteristics as autochorous, anemochorous, or zoochorous. Zoochorous species were further characterized as primarily bird or bat-dispersed based on inspection of their propagules and available literature. Understory species richness and seedling density for trees and shrubs were compared among treatments using a one-way analysis of variance (ANOVA), and between central and edge zones of the plantation plots using paired t-tests.

Plantation understory floristic data were evaluated through correlation and regression analyses, in relation to overstory composition and several structural and environmental variables measured for each plot during the period from 2.5 to 4.5 yr after planting (Table 1). These variables included: total above-ground (overstory) biomass; fine root (< 2 mm diameter) mass in the upper 10 cm of the soil; leaf area index; litter (O-horizon) depth; litter dry mass; and surface soil (0 - 10 cm depth) organic matter.

Overstory above-ground biomass was estimated for each plantation plot at 4.0 years using dimension analysis regressions, based on stem diameter as the dependent variable, developed at this site for each of the three planted species. Measurements of fine root dry mass were obtained at 4.0 yr from 5.1-cm diameter core samples (n = 5 cores/plot) taken to a depth of 10 cm. Soil organic matter content was estimated for each plot at 3.0 yr by loss-on-ignition (at 550 °C) using composite soil samples taken to a depth of 10 cm at five randomly selected points per plot.

Leaf area index (LAI) was measured about every two months at 16 points within each plot between 2.5 and 4.5 yr after plantation establishment. A Li-Cor LAI-2000 Plant Canopy Analyzer was used for these measurements, with all readings taken at 0.3 m above ground level. Plot means for each date were averaged over this 2-yr period for each plot for the purposes of the present study.

Mean litter (O-horizon) depth and dry mass were measured in each plot at 4.5 yr. Litter depth was measured at 25 randomly selected points per plot and mean values calculated. Estimates of forest floor dry mass 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 followed by drying at 65 °C to constant weight.

Results and Discussion

Understory floristic development

During the first two years, ground cover was generally very sparse in the plantations relative to the unplanted control plots, but included most of the grass, herb, and vine species present at the site prior to plantation establishment. Understory colonization by woody species did not occur in any of the plantation or control treatments, with the exception of *Leucaena leucocephala*, seedlings of which were found in several of the plantation plots from the second year onward, the result of natural regeneration by the planted *Leucaena*. Throughout this period the plantations were regularly visited by a number of frugivorous bird species which use the planted trees as roosting sites, and the discarded seeds of bat-dispersed tree species (*Calophyllum brasiliense* and *Terminalia catappa*) were first noted in the plantation alleys after ca. 2 yr.

In spite of apparently regular seed inputs by roosting frugivores, the virtual elimination of understory competition by grasses, and the creation of light, temperature, and humidity conditions favorable for secondary forest species regeneration in the plantation understories from the second year onwards, it was not until just prior to the 2.5-yr survey that such regeneration was first noted in scattered locations within the plantation area. These early colonists included the two bat-dispersed species mentioned above, and *Citharexylum fruticosum*, a bird-dispersed species that is very common in local secondary forests. Thereafter, a rapid increase in both seedling density and species richness occurred in the plantation plots. A very similar temporal pattern was earlier observed in *Albizia lebbek* plantations at this site (Parrotta 1993a).

The apparent delay between the initiation of tree seed inputs and germination does not appear to be due primarily to physical environmental constraints (light, temperature, humidity) but rather to biotic factors responsible for breaking seed dormancy and facilitating germination. Similar observations and analyses of soil fauna and microflora succession made in plantations established on an abandoned pasture site in Costa Rica suggest that delays in natural regeneration by native forest species, despite abundant seed rain, may be linked to the rate of development of fungal and bacterial populations required for breaking seed dormancy (R. Fisher 1994, pers. comm.).

By 4.5 yr, the plantation plots collectively supported a fairly rich understory flora that included 19 species of native and naturalized trees and shrubs, representing 14 families, within the 0.52-ha plot area surveyed (central subplots + edge zones). Most of the seedlings found in the plantations were less than 50 cm in height, and usually less than 30 cm; only a few individuals of *Citharexylum fruticosum* were between 1.5 and 2.0 m tall. In contrast, no woody seedlings were found either in the control plots (total area: 0.08 ha) or elsewhere in the 0.5-ha unplanted, protected grassland surrounding the block

Table 2. Tree and shrub species colonizing study plantation understories.

Species	Family	Fruit type	Disperal agent	Density (No./m^2)
Citharexylum fruticosum	*Verbenaceae*	Fleshy drupe	Birds	7.05
Cordia polycephala	*Boraginaceae*	Fleshy drupe	Birds	4.16
Schinus terebinthifolius	*Anacardiaceae*	Fleshy drupe	Birds	3.23
Calophyllum brasiliense	*Hypericaceae*	Large drupe	Bats	3.03
Terminalia catappa	*Combretaceae*	Large drupe	Bats	0.75
Bourreria succulenta	*Boraginaceae*	Fleshy drupe	Birds	0.75
Spathodea campanulata	*Bignoniaceae*	Dehiscent capsule	Wind	0.53
Bursera simaruba	*Burseraceae*	Drupelike capsule	Birds	0.18
Eugenia pseudopsidium	*Myrtaceae*	Berry	Birds	0.17
Andira inermis	*Papilionaceae*	Large drupe	Bats	0.13
Roystonea borinquena	*Arecaceae*	Slightly fleshy berry	Birds	0.10
Myrcia splendens	*Myrtaceae*	Fleshy berry	Birds	0.09
Ixora ferrea	*Rubiaceae*	Fleshy berry	Birds	0.08
Ocotea coriaceae	*Lauraceae*	Fleshy berry	Birds	0.08
Rauvolfia nitida	*Apocynaceae*	Fleshy drupe	Birds	0.08
Psidium guajava	*Myrtaceae*	Fleshy berry	Birds	0.07
Casearia guianensis	*Flacourtiaceae*	Dehiscent capsule	Birds	0.03
Cedrela odorata	*Meliaceae*	Dehiscent capsule	Wind	0.03
Unidentified taxa				0.07
			Total	20.61

of plantation plots.

Four secondary forest species: *Calophyllum brasiliense*, *Citharexylum fruticosum*, *Cordia polycephala* and *Schinus terebinthifolius*, comprised 85 % of the total number of woody seedlings in the plantation understories (Table 2). A survey of the local tree flora indicated that most of the species encountered as colonists in the plantations could have been derived from parent trees located between 50 and 300 m from the plantation.

The majority (68 %) of the tree and shrub species regenerating within the plantation area are bird-dispersed, their fruits being fleshy drupes or berries containing seeds that are passed through the digestive tract. Three additional species - *Andira inermis, Calophyllum brasiliense*, and *Terminalia catappa*, produce large-seeded drupes dispersed by bats, which carry the fruits to their roosting sites, consume the fleshy outer layers, and drop the uningested seeds. At this site, seeds and seedlings of these chiropterochorous species display a typically clustered distribution, indicating a preference for certain trees as bat roosting sites, usually near the plot edges.

In all, 84 % of the species and 97 % of the total number of seedlings colonizing the plantation understories are zoochorous. As in other moist tropical forest environments, zoochory is the primary diaspore dispersal mechanism for the vast majority of tree and shrub species occurring naturally in the vicinity of this site. The roosting sites provided by the plantation clearly increased the seed rain to the plantation understories relative to the surrounding unplanted grassland areas. The importance of roosting sites for seed inputs into open habitats such as grasslands and mined lands has been demonstrated in several recent studies (Guevara et al. 1986, 1992; McClanahan & Wolfe 1987, 1993).

Only two anemochorous species were found in the plantations: *Cedrela odorata* and *Spathodea campanulata*. Their presence in the plantation understory, and absence in the control plots, into which seeds of these species presumably are also dispersed, suggest that factors in addition to seed rain account for the lack of regeneration of woody species in the grassland surrounding the plantation. At this site, and elsewhere under similar conditions, these regeneration-limiting factors might include competition with grasses and unsuitable microclimatic conditions (Nepstad et al. 1991; Guevara et al. 1992; Parrotta 1992, 1993a; McClanahan & Wolfe 1993).

Plantation overstory and environmental effects

Plantation overstory composition appears to have exerted a considerable influence over both understory species richness and colonization rates by secondary forest species, i.e., seedling density. Significant treatment effects were found with respect to the total number of woody plant species in the plantation understories ($P < 0.05$, ANOVA), with mean species richness ranging from 3.0 ± 0 to 7.7 ± 1.5 species/plot (289 m^2) in the *Casuarina* monoculture (CM) and the *Eucalyptus* +

Table 3. Understory species richness and seedling density for tree and shrub species in plantation understories and control plots 4.5 yr after plantation establishment. Values following means indicate standard error; n = 3 plots per treatment.[1]

Treatment[2]	Primary diaspore dispersal agent: Birds	Bats	Wind	All species
Species richness (No. species/plot[3])				
LM	5.3 ± 1.3^{bc}	1.0 ± 0.7^{abc}	0.3 ± 0.3^{a}	6.7 ± 2.2^{bc}
CM	2.0 ± 0.6^{b}	0.7 ± 0.7^{abc}	0.3 ± 0.3^{a}	3.0 ± 0^{b}
EM	4.3 ± 0.3^{bc}	1.3 ± 0.7^{abc}	1.0 ± 0^{b}	6.7 ± 0.9^{bc}
EL	6.0 ± 1.5^{c}	1.7 ± 0.7^{bc}	0^{a}	7.7 ± 1.5^{c}
EC	2.7 ± 0.7^{bc}	0.7 ± 0.3^{b}	1.3 ± 0.9^{ab}	4.7 ± 1.7^{bc}
CL	2.7 ± 0.7^{bc}	2.3 ± 0.3^{c}	0^{a}	5.0 ± 0.6^{bc}
Control	0^{a}	0^{a}	0^{a}	0^{a}
Seedling density (No./m^2)				
LM	0.271 ± 0.045^{c}	0.023 ± 0.021^{ab}	0.003 ± 0.003^{ab}	0.314 ± 0.026^{d}
CM	0.024 ± 0.019^{ab}	0.006 ± 0.006^{a}	0.001 ± 0.001^{a}	0.031 ± 0.016^{ab}
EM	0.036 ± 0.012^{ab}	0.024 ± 0.018^{ab}	0.012 ± 0.005^{b}	0.072 ± 0.029^{abc}
EL	0.103 ± 0.035^{b}	0.029 ± 0.011^{ab}	0^{a}	0.128 ± 0.046^{c}
EC	0.024 ± 0.005^{a}	0.004 ± 0.002^{a}	0.006 ± 0.004^{ab}	0.034 ± 0.009^{ab}
CL	0.031 ± 0.007^{a}	0.043 ± 0.008^{b}	0^{a}	0.074 ± 0.005^{bc}
Control	0^{a}	0^{a}	0^{a}	0^{a}

[1] Similar superscripts within a column indicate means that were similar within the same seed dispersal mode class ($P < 0.05$, ANOVA). [2] Treatments: LM = *Leucaena leucocephala*, CM = *Casuarina equisetifolia*, EM = *Eucalyptus robusta*, EL = *Eucalyptus* + *Leucaena*, EC = *Eucalyptus* + *Casuarina*, CL = *Casuarina* + *Leucaena*. [3] Plot area = 289 m^2.

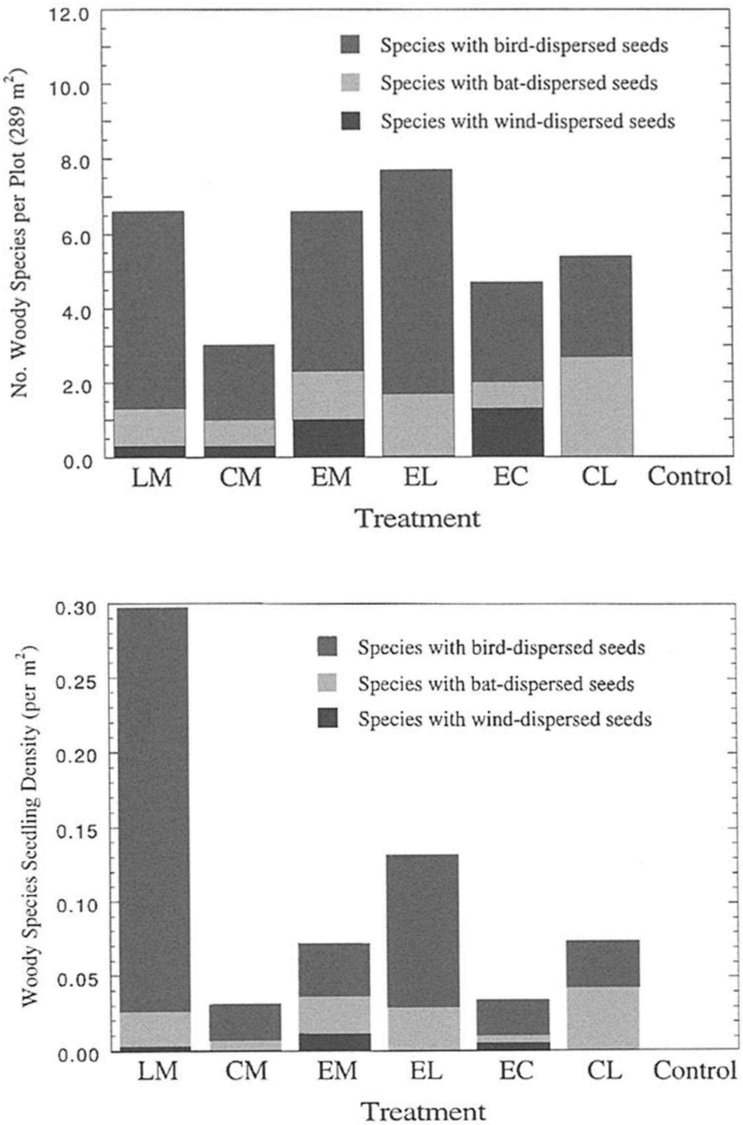

Fig. 1. Understory colonization by native and naturalized secondary forest tree and shrub species 4.5 yr after plantation establishment; treatment averages. **a.** Species richness. **b.** Seedling density. Treatments: LM = *Leucaena leucocephala*, CM = *Casuarina equisetifolia*, EM = *Eucalyptus robusta*, EL = *Eucalyptus* + *Leucaena*, EC = *Eucalyptus* + *Casuarina*, CL = *Casuarina* + *Leucaena*.

Leucaena (EL) treatments, respectively (Table 3).

Similar but somewhat more pronounced trends were found with respect to understory seedling density ($P < 0.0001$, ANOVA), which ranged from 0.031 ± 0.016 to 0.314 ± 0.026 individuals/m^2 in the *Casuarina* and *Leucaena* monoculture treatments, respectively. Treatment effects were not significant for either species richness or seedling density for bat- or wind-dispersed species, but were highly significant for bird-dispersed species, which comprised the majority of colonizing species and total seedling populations in the plantation understories.

The differences among treatments in both species richness and seedling density indicate that *Leucaena* provides the most favorable conditions for understory colonization by secondary forest species, followed by *Eucalyptus* and, finally, *Casuarina*, which supported relatively little understory colonization. In the mixed-species treatments, understory species richness and seedling densities were, in general, intermediate between those of the single-species stands of the two taxa comprising their overstories (Fig. 1).

Of the plantation characteristics and environmental variables examined, significant correlations ($p < 0.05$) were found between understory species richness and litter depth (Fig. 2) and between seedling density and both litter depth and dry mass (Fig. 3). These relationships were negative, with fewer species and lower seedling densities occurring in the understories of plots with greater litter accumulation. Plantation plots with the lowest rates of litter accumulation, in terms of depth and dry mass, included the LM, EL and EM treatments,

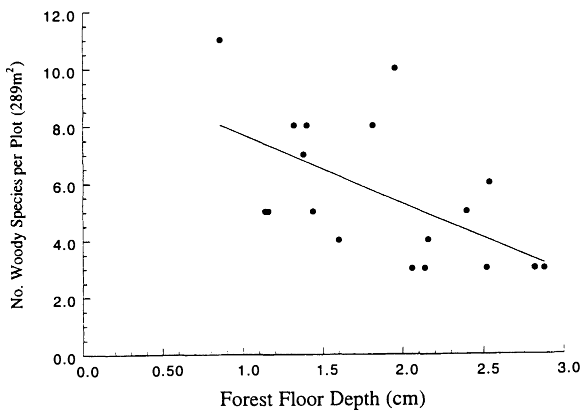

Fig. 2. Relation between understory species richness for colonizing trees and shrubs and forest floor depth at 4.5 yr. $y = 10.1 - 2.4x$ ($r^2 = 0.34$; $F = 8.17$; $P < 0.05$).

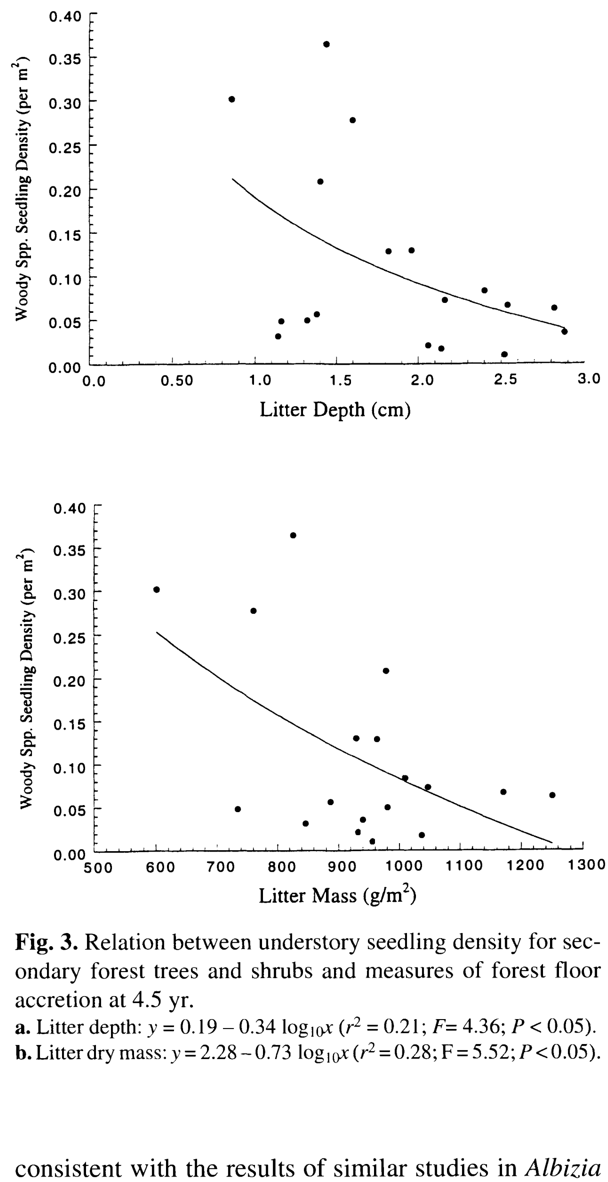

Fig. 3. Relation between understory seedling density for secondary forest trees and shrubs and measures of forest floor accretion at 4.5 yr.
a. Litter depth: $y = 0.19 - 0.34 \log_{10}x$ ($r^2 = 0.21$; $F= 4.36$; $P < 0.05$).
b. Litter dry mass: $y = 2.28 - 0.73 \log_{10}x$ ($r^2 = 0.28$; $F = 5.52$; $P < 0.05$).

while those with higher litter accumulation rates were the EC, CL, and CM treatments (Table 1).

Thus the differences in understory colonization among treatments appear to be strongly related to differences in forest floor depth and dry mass. Within the ranges of litter depth (0.8 - 2.8 cm) and dry mass (600 - 1250 g/m^2) recorded at this site, the data suggest that increased litter accumulation acts as a progressively severe barrier to regeneration by small-seeded (bird-dispersed) tree and shrub species. This does not appear to be the case for large-seeded (bat-dispersed) species. Understory colonization by these species was not influenced by overstory composition as noted earlier, nor were there any significant trends between seedling densities and litter depth or dry mass for these taxa. Apparently, the food reserves present in the seeds of these species are sufficiently large to support development of root systems that can penetrate the litter layer and reach the mineral soil before they are exhausted. There were no indications that leaf litter chemistry, which varies greatly among the three overstory species in this study (and strongly influences litter decomposition rates; author, unpubl.), is influencing understory regeneration through allelopathic interference, as has been suggested by some studies for *Leucaena leucocephala* and *Eucalyptus* spp. (cf. Suresh & Vinaya Rai 1988).

Among the other plantation characteristics and environmental factors analyzed, none were significantly correlated with either understory species richness or seedling density ($P < 0.05$, ANOVA). A suggestive, though not significant ($P = 0.055$, ANOVA), positive correlation was found between species richness and overstory leaf area index of the plantation plots averaged over 12 measurement dates between 2.5 and 4.5 yr. This trend is consistent with the results of similar studies in *Albizia lebbek* plantations at this site that showed a significant negative correlation between seedling density and understory light intensity (Parrotta 1993a).

Plantation edge effects

Comparing understory colonization patterns by secondary forest species between the central and peripheral (edge) zones of the plantation plots, both total species richness and seedling density (Fig. 4) were significantly greater along the edges of the forest plots regardless of overstory composition ($P < 0.001$, *t*-test). These edge effects were significant ($P < 0.001$, *t*-test) for both bird- and bat-dispersed species, though not for wind-dispersed species.

In most plantations, irrespective of overstory composition, trees located along the edges of the plots were

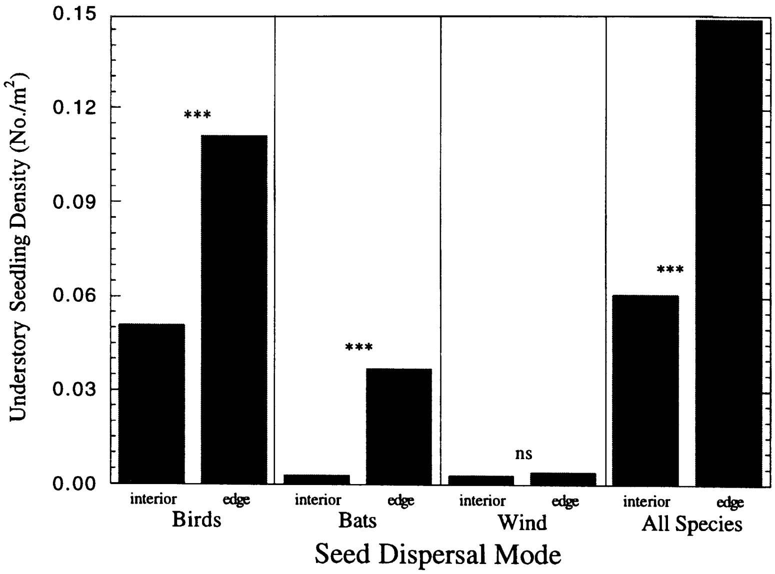

Fig. 4. Comparison of understory seedling densities (colonizing trees and shrubs) in plantation interior and edge zones at 4.5 yr. Statistical comparisons of differences between means (paired t-tests) based on combined data from all plantation plots: *** = $P < 0.001$; ns = not significant.

clearly more attractive as roosting sites for frugivorous bats that transport large-seeded drupes into the experimental area. This is supported by observations of large numbers of discarded seeds along the plot edges relative to the central subplots. A similar preference by frugivorous birds for trees, i.e., roosting sites, along plot border rows is also apparent, although data on seed rain for bird-dispersed species are not available to support this hypothesis. Trees growing along most of the edges of the plantation plots are, in general, larger than those within the central subplots and may therefore provide more accessible perches and/or greater visibility (or echolocation potential, in the case of bats) for roosting frugivores.

Implications for restoration forestry

The results of this study have important implications for the design of plantations that can be used for 'catalyzing' natural forest successional processes, particularly on sites where soil seed banks and rootstocks of native forest species are lacking due to their disturbance histories. The choice of species that will initially form the overstory appears to have, at least in the early stages of development, a significant effect on the numbers of propagules and diversity of zoochorous woody species colonizing the plantation understories.

Tree species that form a thin canopy and produce fine, readily decomposed leaf litter similar to *Leucaena* appear very well suited for this purpose. Such species can create a light- to moderately-shaded understory environment that effectively suppresses the growth of grasses while favoring the germination of many early- and mid-successional tropical forest tree species. Their rapid leaf turnover and decomposition of nutrient-rich litter can result in significant improvements in soil fertility as well as facilitate tree seed germination and seedling development. Due to its high reproductive potential and competitive advantage over native species, however, *Leucaena leucocephala* is not recommended for forest restoration purposes on most sites. Rather, less 'weedy' species with similar architectural traits and litter characteristics that regenerate and compete poorly beneath their own overstory or in surrounding, disturbed, habitats would be preferred. There are numerous such species, especially among the mimosoid legumes, such as *Albizia lebbek*. In contrast, species such as *Casuarina equisetifolia* that tend to form dense crowns casting deep shade in the understory and produce litter that decomposes relatively slowly, and thus create a physical barrier to regeneration by small-seeded secondary forest species, are less likely to yield favorable results.

The importance of frugivorous birds and bats in the colonization of the plantation understories by secondary forest tree and shrub species is also clear from the present study. The behavioral ecology of these critical seed dispersal agents in forest plantation ecosystems merits further study to better explain the understory colonization patterns observed at this site and to provide insights useful for the design of rehabilitation plantations that will attract seed-dispersing wildlife so as to accelerate the rate of introduction of zoochorous propagules and increase understory species biodiversity.

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