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The role of plantation forests in rehabilitating degraded tropical ecosystems

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ABSTRACT

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Plantations of multi-purpose tree species can play an important role in restoring productivity, ecosystem stability, and biological diversity to degraded tropical lands. The present study, conducted at a degraded coastal pasture site in Puerto Rico, compares 4.5-year-old *Albizia lebbek* (L.) Benth. plantation stands and adjacent control areas with respect to biomass production, understorey species diversity and nutrient storage patterns within vegetation, forest floor organic matter, and mineral soil compartments.

Mineral soil (0–20 cm depth) organic carbon (OC) and total nitrogen (TN) were both significantly higher in plantation plots (1.70% OC, 0.095% TN) than in control plots (1.44% OC, 0.074% TN), while available phosphate and exchangeable cations were similar between treatments.

Standing crop biomass of understorey vegetation, forest floor organic matter and fine (less than 2 mm) roots averaged 160 g m^{-2}, 349 g m^{-2}, and 362 g m^{-2} in the plantation plots and 420 g m^{-2}, 311 g m^{-2}, and 105 g m^{-2} in the control plots. Nitrogen concentrations within each of these biomass components were, however, consistently higher in the plantation plots. Plantation understorey species appear to be efficient 'scavengers' of biologically fixed nitrogen, and appear to help buffer the system against leaching losses.

Species richness was considerably greater in plantation than control plots for grasses, vines, and forbs. Seedlings of several secondary forest species were abundant in the plantation understorey but absent in control plots, suggesting an important role for such plantations in accelerating natural regeneration of native forest species on certain sites.

INTRODUCTION

Environmental degradation is proceeding at an unprecedented rate in many tropical regions, jeopardizing prospects for conservation of biological diversity and sustainable economic development of agricultural and forest resources. Each year, an estimated 11.1 million ha of tropical forests and woodlands are destroyed or seriously degraded through agricultural expansion, logging, and fuelwood collection (Lanly, 1982; World Resources Institute/

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International Institute for Environment and Development (IIED), 1988). Desertification, the process of degradation in arid, semiarid, and subhumid regions, has been exacerbated in many areas by increases in human and livestock pressures beyond the natural carrying capacities of these lands. Severe soil erosion renders unproductive an estimated 6–7 million ha of agricultural land each year (World Resources Institute/IIED, 1988). Waterlogging, salinization, and alkalinization, reduce the productivity of an additional 1.5 million ha of irrigated cropland each year (Kovda, 1983).

Until recently, the most common response to land degradation has been abandonment. Short periods of abandonment of temporarily degraded lands have been the basis of traditional shifting cultivation, nomadic pastoralism and transhumance systems. The long-term viability of such agricultural systems requires that fallow periods exceed the time needed for the land to recover from the tree felling, farming, grazing, or other disturbance. Under conditions of increasing population density or intensified land-use, fallow periods are often shortened, or eliminated. Without adequate inputs such as plant nutrients, productivity and land utility commonly decline, often precipitously as in the case of pasture development in the Amazon basin (Uhl et al., 1988). Where abandonment is not a viable or desirable option because of land shortage or the need to conserve the ecological integrity of neighboring fragile ecosystems, human intervention may be required to recover sustainable productivity.

Degraded lands are typically characterized by impoverished or eroded soils, hydrologic instability, reduced primary productivity and diminished biological diversity. An important goal of ecological rehabilitation is to accelerate natural successional processes so as to increase biological productivity, reduce rates of soil erosion, increase soil fertility (including soil organic matter), and increase biotic control over biogeochemical fluxes within the recovering ecosystem. Given the initial human investments required for rehabilitation, it may also be necessary to manage rehabilitating ecosystems for early economic returns without jeopardizing or unduly slowing recovery processes.

Forest plantations, using appropriate tree and shrub species, can play an important role in the tropical ecosystem rehabilitation. A number of recent studies have demonstrated that plantations of native or exotic species adapted to the stressful conditions characteristic of degraded lands can reverse degradation processes by stabilizing soils through development of extensive root systems, increasing soil organic matter through enhancement of aboveground litter production (Lowry et al., 1988), fine root turnover and decomposition rates (Montagnini and Sancho, 1990), moderation of soil pH and improvement of soil nutrient status (Sanchez et al., 1985; Chakraborty and Chakraborty, 1989).

The development of a plantation canopy can alter the understorey microclimate and the soil physical and chemical environment so as to facilitate recruitment, survival and growth of native forest species which otherwise would only very slowly, if ever, regenerate on degraded sites (Uhl et al., 1982; Prasad and Pandey, 1989; Soni et al., 1989). Thus, plantations may act as 'foster ecosystems' (Lugo, 1988), accelerating development of genetic and biochemical diversity on degraded sites (Verma et al., 1982).

The choice of plantation species is likely to greatly influence both the rate and trajectory of rehabilitation processes. Among species that may be considered suitable for a given degraded site, there may be considerable variations in their capacity to stabilize soils, increase soil organic matter and available soil nutrients (Gill et al., 1987; Sharma and Gupta, 1989) and facilitate understorey development (Somarriba, 1988; Pande et al., 1988). These variables include susceptibility to pests and diseases, patterns of aboveground and root biomass accumulation (Jonsson et al., 1988; Parrotta, 1989), nutrient utilization and allocation, litter production and fine root turnover, and rates of litter decomposition, greatly influenced by litter chemistry (O'Connell, 1986; Gill et al., 1987) and the presence of secondary compounds that may inhibit the activity of decomposing organisms (Suresh and Vinaya Rai, 1988). Nitrogen-fixing species inoculated with effective strains of *Rhizobium* or *Frankia* can have a dramatic effect on soil fertility through their production of readily decomposed, nitrogen-rich litter and turnover of fine roots and nodules (Bernhard-Reversat, 1988; Montagnini and Sancho, 1990). *Albizia lebbek* (L.) Benth., commonly known as siris, a nitrogen-fixing, leguminous, multi-purpose tree native to South Asia and naturalized in many tropical regions, exhibits a number of characteristics that make it a good candidate for restoration of degraded tropical lands. The tree grows well in semiarid and moist tropical and subtropical regions under a wide range of edaphic conditions, including saline, alkaline, and very rocky or sandy soils. Currently used in a variety of agroforestry systems, it is an excellent source of small timber, fuelwood, livestock fodder, tannins, gums and traditional medicinal products (Parrotta, 1987a).

The present study, conducted at a degraded coastal pasture site in Puerto Rico, compares 4.5-year-old plantations of *Albizia lebbek*, and control areas with respect to aboveground and belowground biomass production, vegetation and soil nutrient storage patterns, and understorey community structure.

SITE DESCRIPTION

The investigation was conducted at the University of Puerto Rico's experimental farm in Toa Baja, located on the northern coast of the island (66° 10′W, 18°27′N). Rainfall at the site averages 1600 mm per year, 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, moderately alkaline (pH 7.9–8.4), calcareous sands of marine origin (isohypothermic Typic Troposamments). Once part of a coastal dune system, soils and vegetation at the site have been subject to frequent, often severe disturbances in recent decades, including cultivation and large-scale soil perturbations such as sand extraction and leveling. For approximately 2–3 years prior to plantation establishment, the site had been subjected to moderate grazing and occasional small-scale fires. At the time of establishment of experimental plantations in 1984, the site was dominated by grasses, principally *Panicum maximum* Jacq. and *Tricholaena repens* (Willd.) Hitch., and a variety of forbs; woody plants were absent.

Two months prior to the start of the experiment, the experimental area was cultivated using a disk harrow. In December 1984, plantation and control plots were established using a randomized block experimental design, each of three blocks containing one replicate plot of three tree spacing treatments and a control. In the plantation plots, 324 4-month-old, containerized *Albizia lebbek* seedlings were planted at spacings of either 2 m×2 m, 1 m×1 m, or 0.5 m×0.5 m. Plot size varied depending on tree spacing: 1296 m^2, 324 m^2, and 81 m^2, for the low, intermediate and high density treatments, respectively, and 200 m^2 (10 m×20 m) for the control plots. After planting, the site was protected from grazing and fire for the duration of the study. Approximately every 2 months during the first year of the experiment, plantation plots were manually weeded. Plantation plots were neither irrigated nor fertilized.

MATERIALS AND METHODS

In May 1989, 4.5 years after plantation establishment, aboveground and coarse root (greater than 1 cm diameter) biomass of the tree crop (*Albizia lebbek*) was estimated from dimension analysis regressions relating dry mass to height and basal diameter. These equations were developed by harvesting and measuring trees in a representative range of size classes from within all plantation plots (Table 1). Using height and basal diameter data recorded for all trees in the interior 10 × 10 tree subplot of each plantation plot, biomass estimates for leaves, branches and stems (three size classes), and coarse roots in each of the nine plantation plots were calculated as the sum of the individual tree estimates for each biomass component.

Trees harvested for the development of biomass regressions were separated into several biomass classes, and weighed in the field. Subsamples of leaf biomass and randomly selected branch and stem segments from each size category were returned to the laboratory for dry mass conversion, evaluation of wood-to-bark ratios, and nutrient analyses.

Floristic composition, aboveground biomass, litter (forest floor biomass), and root biomass in control areas and in the plantation understorey were measured in 1 m×1 m quadrats. In the control areas, separated from the plantation plots by a buffer zone 5 m in width, a total of 15 quadrats were

TABLE 1

Equations used to estimate *Albizia lebbek* aboveground and coarse root biomass in plantation plots

Biomass component	n	Equation	r^2	CV	F
Leaves	36	$\log_{10}Y=-2.41+1.21\ast(\log_{10}D^2)$	0.948	39.7	618
Branches/stems					
<1 cm	36	$\log_{10}Y=-2.38+1.11\ast(\log_{10}D^2)$	0.914	35.6	360
1–2.5 cm	36	$Y=-0.796+0.0741\ast(D^2)-0.139\ast(DH)$ $+0.915\ast(H)-0.700\ast(\log_{10}D^2H)$	0.920	37.0	90
>2.5 cm	32	$Y=-2.99+0.434\ast(\log_{10}D^2H)-0.0131\ast(DH)$ $-5.87\ast(D)-0.00934\ast(D^2H)$	0.984	15.7	417
Roots >1 cm	20	$Y=0.0539+0.0102\ast(D^2H)$	0.992	18.9	2327

Notes: Regressions based on 36 trees harvested from within plantation plots. The mean height of sample trees (±SE) was 5.2±0.4 m, mean basal diameter (±SE) was 8.0±0.8 cm.
Y is oven-dry mass (kg); *H* is tree height (m); *D* is basal diameter (cm).

located randomly. In the plantation plots, 21 quadrats were established, four in each of the low density plots, two in each of the intermediate density plots, and one in each of the high density plots. Within plantation plots, quadrats were located randomly within a central 10 × 10 tree subplot to avoid possible edge effects.

Prior to harvest, all species occurring in each quadrat were identified and, for woody seedlings, height and basal diameters recorded. All live plant material was harvested and separated by life form (grasses, vines and forbs, woody seedlings). Leaf, wood and bark litter retained by a 1.0 mm sieve was collected from a central 0.5 m×0.5 m area within each quadrat. Standing biomass of fine and small roots (less than 2 mm and 2–10 mm diameter, respectively) was measured to a depth of 40 cm at 10-cm intervals by collecting, by hand and sieving, all roots in a 30 cm×30 cm pit dug from the center of each quadrat.

A composite mineral soil sample comprised of three 20 cm cores was taken within each quadrat using a tube sampler 1.4 cm in diameter. Ten additional 20 cm cores were taken in both the control and plantation plots for bulk density measurements using a tube sampler 5.1 cm in diameter. In June–July 1990, 13 months after the preceding measurements were made, nitrogen mineralization was measured over a 22-day period at ten locations in both plantation and control plots to a depth of 30 cm by in situ incubation of relatively undisturbed, covered, plastic soil cores 5.1 cm in diameter (Anderson and Ingram, 1987), 2 M KCl extraction of the fine (less than 2 mm) soil fraction, and colorimetric determination of nitrate and ammonium (Keeney and Nelson, 1982).

All aboveground biomass, forest floor, and root samples were dried at 65°C to constant weight prior to nutrient analyses, with subsamples dried at 105°C or combusted at 550°C for oven-dry weight and ash-free dry weight conversion factors, respectively. Samples of *Albizia lebbek* branch and stem components were separated into wood and bark fractions to determine wood-to-bark ratios and for subsequent nutrient analyses.

Plant tissue samples were analyzed for nitrogen and carbon content using a Carlo Erba Elemental Analyzer. Potassium, magnesium, and calcium concentrations in plant tissue samples were measured by atomic absorption spectrophotometry following wet digestion at 250°C in concentrated HNO_3, H_2SO_4, and H_2O_2 (Luh Huang and Schulte, 1985). Phosphorus concentrations were determined using a spectrophotometer by the ascorbic acid method (Watanabe and Olsen, 1965) following the wet digestion procedure described above.

Soils were air-dried at 40°C prior to nutrient analysis. Subsamples of soil were dried to constant weight at 105°C to determine air-dry to oven-dry conversion factors used to correct results of soil nutrient analyses performed on air-dried soils. Soil pH was determined with a Fisher Acumet glass electrode using a 1:2.5 suspension of soil with deionized water. Organic carbon was determined by the Walkley–Black method (Nelson and Sommers, 1982). Measurements of total Kjeldahl nitrogen were made using standard digestion and colorimetric techniques (Wilde et al., 1979). Exchangeable cations were determined by atomic absorption spectrophotometry following extraction with ammonium acetate at pH 7.0 (Thomas, 1982). Available phosphate was determined colorimetrically (Watanabe and Olsen, 1965) following a sodium bicarbonate extraction at pH 8.5 (Olsen and Sommers, 1982).

RESULTS AND DISCUSSION

Biomass accumulation

At the time the present study was conducted, the plantation plots were characterized by a continuous *Albizia lebbek* canopy with a mean leaf area index of 3.8. Mean tree height, mean stem basal diameter, and total basal area averaged 4.0 m, 5.5 cm, and 28.7 m^2 ha^{-1}, respectively, across all density treatments.

Live aboveground biomass in the plantation plots was estimated to be 4660 g m^{-2} (Table 2). *Albizia* stems and branches (4110 g m^{-2}) and leaves (380 g m^{-2}) comprised 96.4% of the total. Understorey vegetation (grasses, forbs and vines, woody seedlings) averaged 160 g m^{-2}. In contrast, live aboveground biomass in the control averaged 420 g m^{-2}, significantly higher than plantation understorey biomass, but only 9.0% of the total live aboveground biomass in the plantation. In the control, understorey live aboveground biomass was dominated by grasses (312 g m^{-2}), which comprised an average of 74% of the total. In the plantation understorey, the biomass of grasses aver-

TABLE 2

Mean (± standard error) plant dry mass in *Albizia lebbek* plantation plots and adjacent control area 4.5 years after plantation establishment

Biomass category	Standing biomass ($g\ m^{-2}$)	
	Plantation	Control
Aboveground biomass		
Albizia lebbek		
Leaves	380±110	0
Branches/stems		
<1 cm	220±50	0
1–2.5 cm	820±210	0
>2.5 cm	3070±470	0
Total *Albizia*	(4500±840)	(0)
Understorey vegetation		
Grasses	96±27	312±72
Vines/forbs	47±20	108±24
Woody seedlings	17±7	0
Total understorey	(160±25)	(420±61)
Total aboveground biomass	4660±1430	420±61
Belowground biomass		
Roots		
Fine (<2 mm)	362±32	105±14
Small (0.2–1 cm)	246±68	23±11
Coarse (>1 cm)	2115±648	0
Total roots	(2723±729)	(129±21)
Forest floor (litter)	349±45	311±61
Total belowground biomass	3072±723	440±72
Total above- and belowground biomass	7718±2149	860±124

Notes: $n=9$ for all plantation mean values: grand means of each of three replicate plots for each density treatment for each parameter. See text for further explanation.
$n=15$ for all control plot mean values: based on 1 m × 1 m quadrat data.

aged only 96 $g\ m^{-2}$, and comprised somewhat less (60%) of the total live aboveground biomass than in the control.

There were marked differences between the control and plantation systems with respect to root distribution in terms of total root mass, size class distribution, and depth distribution. Mean total root mass in the plantation plots was 2710 $g\ m^{-2}$ vs. 129 $g\ m^{-2}$ in the control. Coarse roots, absent in the control, comprised 78% of total root mass in the plantation plots. Small and fine root biomass were both significantly greater in the plantation plots than in the control (Table 2). In the control area, fine roots were not encountered below 30 cm depth, and 79% of the total fine root biomass occurred in the 0–10 cm stratum. In the plantation plots, fine roots were encountered to a depth of 40 cm, with 54% of the total biomass occurring in the 0–10 cm stratum. In contrast to fine roots, small roots tended to be more uniformly distributed through the soil profile, and were most abundant in the 10–20 cm and 20–30 cm strata of the plantation plots, but did not occur below 20 cm in the control. Differences in root biomass and depth distribution between the plantation and control treatments may be attributed to the dominance and root system morphology of the tree crop in the former. The majority of fine roots and nearly all roots more than 0.2 cm in diameter harvested from the plantation plots were identified as *Albizia*.

Floristic composition

A total of 44 species were recorded in plantation and control quadrats, including 11 species of secondary forest trees, 11 species of vines, 18 species of forbs, and four grass species. Seedlings of an additional 16 tree and shrub species were found within the plantation plots but were not recorded in the quadrats; no forest tree species were found in the control area.

Species richness for all life forms was considerably greater in the plantation plots, particularly for woody seedlings and vines (Fig. 1). Seedlings of secondary forest tree and shrub species, were abundant in the plantation plots, with a mean density of 1.14 seedlings m^{-2} for all species. The most common tree species found in the plantation understorey were *Citharexylum fruticosum* L. (pasture fiddlewood), *Spathodea campanulata* Beauv. (African tulip tree), and *Eugenia monticola* (Sw.) DC. (black cherry); *Albizia lebbek*

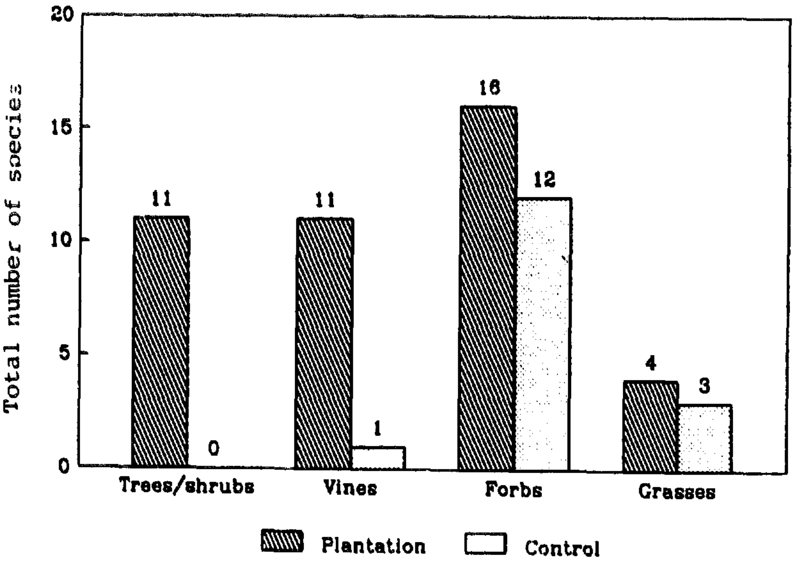

Fig. 1. Species richness in plantation understorey and in control plots (total sampling area: 21 m^2 in plantation and 15 m^2 in control plots).

seedlings were relatively uncommon, despite abundant seed rain to the forest floor since plantation establishment.

Several interrelated factors may account for the relative floristic richness of the plantation plots. Studies of succession in Amazonian forest ecosystems following human disturbance (Uhl et al., 1982, 1988; Uhl, 1987; Nepstad and Uhl, 1991) have suggested a number of barriers to natural regeneration of forest tree species on degraded sites applicable to the present study. Such barriers include low propagule availability (seeds, root stocks), seed predation, non-availability of suitable microhabitats for plant establishment, low soil nutrient availability, seedling predation, seasonal drought, and root competition with old field vegetation.

Canopy development in the plantation appears to have indirectly increased propagule (seed) availability by providing roosting and nesting sites for a variety of birds, including several seed- and fruit-eating species. Of the tree and shrub species occurring in the plantation, at least four, including the most common, *Citharexylum fruticosum*, produce seeds characteristically dispersed by birds. Similarly, the seeds of the woody vine *Passiflora edulis* Sims (passion fruit) are commonly bird-dispersed. For large-seeded tree species such as *Calophyllum brasiliense* Camb., bats are the likely dispersal agents; the clumped distribution of *Calophyllum* seedlings observed within the plantation supports this hypothesis. The presence in the plantation understorey, and absence in the control, of tree species with wind-dispersed seeds (e.g. *Spathodea campanulata*) is probably because of factors other than seed availability such as microhabitat availability, relative lack of root competition with grasses, and perhaps more optimal soil moisture and nutrient conditions. Shading by the tree crop may have increased rates of germination, survival, and growth for tree, shrub, vine, and forb species through suppression of grass growth, reduced light intensity and increased humidity in the understorey.

System nutrient distribution and soil fertility

Plant tissue nutrient concentrations varied both among vegetation components and between plantation and control treatments (Table 3). Among biomass components common to both plantation and control treatments (grasses, vines/forbs, fine roots and forest floor), nutrient concentrations in the plantation were often markedly higher than in the control. The 2.2-fold increase in vine/forb nitrogen concentrations in the plantation vs. the control is striking, given the floristic similarities between treatments with respect to forb species (which dominated dry mass in the vine/forb category). It is hypothesized that at least some of the dominant understorey species common to both treatments exhibit considerable plasticity with respect to nutrient uptake, and that increased nitrogen concentrations in these species are a reflection of

TABLE 3

Mean (±standard error) nutrient concentrations in plant tissues in experimental plantation plots and control areas

	n	Mean concentration (% ash-free dry wt.)						
		C	N	n	P	K	Ca	Mg
Albizia lebbek								
Leaves	34	50.8±0.5	4.15±0.11	5	0.124±0.017	2.05±0.16	1.44±0.15	0.53±0.03
Twigs < 1 cm								
Wood	7	45.1±0.1	0.96±0.20	3	0.059±0.28	0.85±0.17	1.12±0.67	0.26±0.06
Bark	8	46.0±2.0	2.03±0.26	3	0.072±0.013	1.93±0.16	2.23±0.66	0.72±0.17
Branches/stems								
1-2.5 cm								
Wood	7	46.2±0.1	0.41±0.03	3	0.021±0.004	0.59±0.10	0.41±0.15	0.065±0.003
Bark	9	47.4±0.6	2.38±0.17	3	0.027±0.003	0.91±0.02	2.23±0.37	0.223±0.003
> 2.5 cm								
Wood	24	45.9±0.2	0.26±0.03	6	0.013±0.001	0.69±0.07	0.29±0.01	0.027±0.003
Bark	24	47.7±0.3	1.97±0.06	4	0.042±0.004	1.32±0.13	1.60±0.12	0.129±0.028
Understorey vegetation								
Grasses								
Plantation	12	45.4±0.4	2.04±0.10	8	0.096±0.010	1.81±0.44	1.40±0.28	0.76±0.20
Control	12	46.2±0.4	0.97±0.08	8	0.047±0.004	1.87±0.34	1.20±0.08	0.40±0.06
Vines/forbs								
Plantation	12	48.6±0.9	2.83±0.11	8	0.152±0.017	3.15±0.46	2.75±0.35	0.64±0.04
Control	12	44.1±0.7	1.27±0.13	8	0.064±0.008	2.78±0.33	1.99±0.29	0.38±0.03
Woody spp.								
Plantation	8	43.2±1.3	1.87±0.17	4	0.075±0.14	1.51±0.21	1.78±0.27	0.48±0.19
Forest floor								
Plantation	12	57.6±1.1	3.34±0.15	8	0.072±0.007	0.58±0.08	5.01±0.94	0.75±0.08
Control	12	54.6±2.8	1.90±0.11	8	0.066±0.008	0.80±0.18	3.83±0.87	0.51±0.06
Roots								
Fine (< 2mm)								
Plantation	20	53.3±0.4	2.49±0.11	5	0.067±0.006	2.39±0.69	2.40±0.28	0.53±0.02
Control	15	53.6±0.9	2.12±0.13	5	0.072±0.008	1.21±0.13	3.26±0.42	0.65±0.09
Small (0.2-1 cm)	21	50.0±0.9	1.91±0.10	4	0.053±0.011	1.88±0.59	1.56±0.03	0.21±0.02
Coarse (> 1 cm)	10	48.8±1.2	1.60±0.15	4	0.020±0.002	0.97±0.17	0.93±0.18	0.10±0.03

greater nitrogen availability in the plantation. The relatively high nitrogen concentrations in fine root and forest floor biomass categories in the plantations appear to be related to the predominance of nitrogen rich *Albizia* leaf litter and fine roots within these components.

Plantation soils were markedly enriched in total nitrogen and organic carbon relative to the control, while exchangeable cations and available phosphate concentrations were similar between treatments (Table 4). Prior to plantation establishment, mean nitrogen and organic carbon concentrations in the mineral soil (of both plantation and control areas) were 0.070% and 2.18%, respectively. Two years after plantation establishment, mineral soil nitrogen and organic carbon concentrations averaged 0.087% and 1.68% in the plantation, and 0.086% and 1.79% in the control. The sharp, early decline

TABLE 4

Mean values (± standard error) of properties of surface soils (0–20 cm) in plantation and control plots 4.5 years after plantation establishment

	Plantation	Control
Bulk density (g cm^{-3})	1.04 ±0.03	1.07 ±0.02
pH	8.35 ±0.11	8.24 ±0.07
Organic carbon (%)	1.70 ±0.12	1.44 ±0.17
Total nitrogen (%)	0.095±0.006	0.074±0.010
C:N	17.9	19.5
Available phosphate (μg g^{-1})	61 ±10	52 ±11
Exchangeable cations (mEq per 100 g)		
Potassium	0.065±0.003	0.058±0.004
Sodium	0.092±0.005	0.079±0.002
Calcium	24.8 ±1.2	25.6 ±4.2
Magnesium	1.37 ±0.11	1.43 ±0.13

Notes: $n=10$ for bulk density and pH, respectively, for both plantation and control plots; $n=21$ (plantation) and 15 (control) for mean organic carbon and total nitrogen values; $n=9$ (plantation) and 3 (control) for mean available phosphate and exchangeable cations values. See text for further explanation.

in soil organic carbon and rise in soil nitrogen may have been related to the acceleration of organic matter decomposition following site preparation prior to plantation establishment (Parrotta, 1987b). Between 2.0 and 4.5 years, soil organic carbon continued to decline in the control area while remaining unchanged in the plantation at approximately 78% of the pre-plantation level. After an initial increase in both the plantation and control, soil nitrogen concentrations appear to have declined to pre-plantation levels in the control and increased in the plantation to approximately 36% above pre-plantation levels.

These data suggest that *Albizia* and its understorey associates have had a significant, positive effect on soil nitrogen and carbon in comparison with the control. Biological nitrogen fixation of atmospheric nitrogen by *Rhizobium*, the production and turnover of relatively nitrogen-rich leaf litter, and fine roots in the plantation are plausible explanations of the differences observed between treatments in mineral soil carbon and nitrogen content.

Soil pH was slightly, though not significantly, higher in the plantation than in the control treatment, with mean values of 8.35 and 8.24, respectively. These values are comparable to pre-plantation data. There was no difference of soil bulk density between the treatments.

Mean nitrogen mineralization, measured as total nitrate+ammonium-N produced during a 22-day in situ incubation to 30 cm depth, was approximately 39% greater in the plantation (8 1 μg g^{-1} soil) than in the control (5.8

μg g^{-1} soil; Table 5). Most mineral nitrogen produced was nitrate-N, in agreement with studies from a variety of dry tropical forest soils (Wetselaar, 1980; Bernhard-Reversat, 1981; Pereira, 1982). Expressed as a percentage of total soil nitrogen, mineral nitrogen production in the 0–20 cm strata during this 22-day period was similar between treatments, approximately 0.85% and 0.84% in the plantation and control, respectively.

System carbon and nitrogen storage patterns were markedly different between plantation and control plots, reflecting treatment differences in vegetation dry mass and differences in carbon and nitrogen concentrations among vegetation and soil components (Table 6, Fig. 2). Carbon stores in the plantation were 90% greater than in the control at 4.5 years (6.496 vs. 3.412 kg m^{-2}). Aboveground *Albizia* biomass accounted for approximately 2.05 kg carbon m^{-2}, or 66% of the difference between plantation and control carbon stores. Differences in belowground carbon stores between treatments were also great (4.382 kg ha^{-1} in the plantation, 3.242 kg m^{-2} in the control), with mineral soil organic carbon comprising 41% of the difference in total belowground stores.

Similar patterns were found with respect to total nitrogen stores at 4.5 years. Relative to the control, plantation nitrogen stores were approximately 64% higher (275.8 vs. 167.8 g m^{-2}). Aboveground nitrogen stores were more than 11 times greater in the plantation than in the control (44.1 vs. 3.9 g m^{-2}), with *Albizia* biomass comprising 93% of the total aboveground stores in the plantation. In spite of marked differences in understorey biomass between treatments, the total nitrogen content of the plantation understorey vegetation was similar to that of the control, a reflection of the higher nitrogen concentrations in plantation understorey vegetation, as discussed above. Mineral soil nitrogen stores (157.6 g m^{-2}) comprised 96% of the belowground total in the control, with roots (2.1 g m^{-2}) and forest floor biomass (4.2 g m^{-2}) comprising the remainder. In the plantation, mineral soil nitrogen (197.8 g m^{-2}) comprised 85.4%, roots 11.0%, and forest floor biomass 3.6% of the belowground total.

These data indicate that relative to the control, the plantation system has

TABLE 5

Mean nitrogen mineralization during 22-day in situ incubation (μg N g^{-1} soil ± standard error; $n=10$)

Soil depth (cm)	*Albizia* plantation			Control		
	NO_3-N	NH_4-N	NO_3+NH_4-N	NO_3-N	NH_4-N	NO_3+NH_4-N
0–10	15.2±2.0	1.0±0.3	16.2±2.0	13.2±1.8	0.1±0.3	13.3±1.8
10–20	4.7±1.4	0.5±0.2	5.1±1.5	2.1±0.5	0.4±0.1	2.6±0.5
20–30	2.8±0.9	0.2±0.2	2.9±1.0	1.5±0.8	0.1±0.2	1.5±0.8

TABLE 6

Estimated system nutrient standing stocks (g m^{-2}) in *Albizia lebbek* plantation plots and adjacent control area 4.5 years after plantation establishment

	Plantation						Control					
	C	N	P	K	Ca	Mg	C	N	P	K	Ca	Mg
Aboveground biomass												
Albizia lebbek												
Leaves	181	14.8	0.44	7.3	5.1	1.90	0	0	0	0	0	0
Twigs < 1 cm	96	2.9	0.13	2.7	3.3	0.93	0	0	0	0	0	0
Branches/stems												
1–2.5 cm	365	6.8	0.18	3.3	6.5	0.80	0	0	0	0	0	0
> 2.5 cm	1406	16.3	0.52	24.0	15.0	1.35	0	0	0	0	0	0
Total *Albizia*	(2048)	(40.8)	(1.27)	(37.3)	(29.9)	(4.98)	(0)	(0)	(0)	(0)	(0)	(0)
Understorey vegetation												
Grasses	39	1.8	0.08	1.6	1.2	0.65	128	2.7	0.13	5.2	3.3	1.12
Vines/forbs	20	1.2	0.06	1.3	1.1	0.26	42	1.2	0.06	2.6	1.9	0.36
Woody seedlings	7	0.3	0.01	0.2	0.3	0.08	0	0	0	0	0	0
Total understorey	(66)	(3.3)	(0.15)	(3.1)	(2.6)	(0.99)	(170)	(3.9)	(0.19)	(7.8)	(5.2)	(1.48)
Total aboveground biomass	2114	44.1	1.42	40.4	32.5	5.97	170	3.9	0.19	7.8	5.2	1.48
Belowground biomass and soil												
Roots												
Fine (< 2 mm)	146	6.8	0.19	6.6	6.6	1.45	43	1.7	0.06	1.0	2.6	0.52
Small (0.2–1 cm)	108	4.1	0.12	4.1	3.4	0.46	11	0.4	0.01	0.4	0.3	0.05
Coarse (> 1 cm)	445	14.6	0.18	8.9	8.5	0.94	0	0	0	0	0	0
Total roots	(700)	(25.6)	(0.49)	(19.5)	(18.5)	(2.86)	(54)	(2.1)	(0.07)	(1.4)	(2.9)	(0.57)
Forest floor	143	8.3	0.18	1.4	12.4	1.85	121	4.2	0.15	1.8	8.5	1.12
Mineral soil (0–20 cm)	3539	197.8	4.10	5.3	1033.0	34.51	3067	157.6	3.60	4.8	1090.0	36.86
Total belowground	4382	231.7	4.77	26.2	1063.9	39.22	3242	163.9	3.82	8.0	1101.4	38.55
System totals	6496	275.8	6.19	66.6	1096.4	45.19	3412	167.8	4.01	15.8	1106.6	40.03

Notes: For branch and stem components, total nutrient content estimated as the product of total biomass (wood and bark) and weighted average nutrient concentration. Bark comprised an average of 41.0%, 23.6%, and 16.4% of the total dry mass for the < 1 cm, 1–2.5 cm, and > 2.5 cm branch/stem size classes, respectively. Soil nutrient stores based on figures presented in Table 3: total nitrogen and carbon, available phosphorus, exchangeable potassium, calcium, and magnesium.

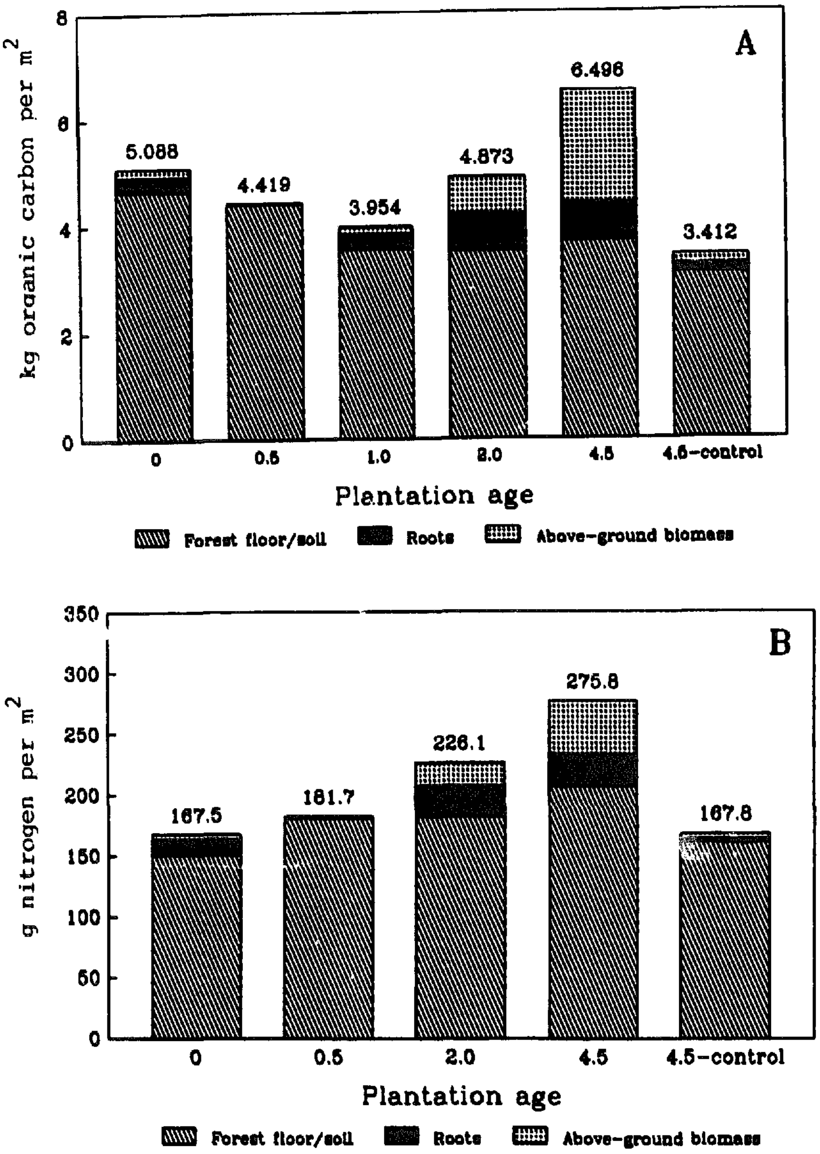

Fig. 2. Total carbon and nitrogen stores in *Albizia* plantation system during first 4.5 years of development: (A) organic carbon; (B) total nitrogen.

accumulated approximately 3.08 kg m^{-2} of carbon and 108 g m^{-2} of nitrogen during a 4.5 year period, a mean annual gain of approximately 0.69 kg m^{-2} for carbon, and 24 g m^{-2} for nitrogen. As indicated in Fig. 2(a), carbon stores declined dramatically during the first year of plantation development, a decline due almost entirely to soil carbon losses. Increases in plantation system carbon stores between 1.0 and 4.5 years, averaging 0.73 kg m^{-2} year^{-1}, were the result of carbon storage in vegetation, principally the tree crop. In contrast, the plantation system accumulated nitrogen at a fairly constant rate from the time of plantation establishment in both soil and vegetation compartments (Fig. 2(b)).

In their extensive review of carbon storage patterns in tropical forest ecosystems, Brown and Lugo (1982) reported a mean total carbon storage estimate of 54.5 kg m^{-2} for 14 mature lowland tropical moist forest systems. Given the organic carbon accumulation rates estimated in the present study, the plantation system would require approximately 74 years to attain organic carbon stores comparable to the value cited above for mature lowland moist forests. While it may be unreasonable to extrapolate the short-term data from the present study, the above comparison does suggest that organic carbon is increasing at a rate which could lead to carbon storage patterns comparable to natural forest systems within a foreseeable period of time.

Rates of system nitrogen accumulation in the present study (24 g m^{-2} $year^{-1}$) compare favorably with estimates from studies of successional tropical forest systems. Early successional forests in the tropics reportedly accumulate nitrogen at an average annual rate of approximately 12 to 15 g m^{-2}, of which an estimated 10 g m^{-2} is stored in vegetation (Greenland, 1975) and from 2 to 5 g m^{-2} in soils (Greenland and Nye, 1959). While rates of biological nitrogen fixation by *Albizia lebbek* (in symbiosis with *Rhizobium*) have not been quantified in the present study, the rapid rate of nitrogen accumulation in the plantation relative to the control strongly suggests the importance of this process in the plantation system and its role in ecosystem rehabilitation at this site.

Rehabilitation processes and management implications

The observed patterns of biomass production, carbon and nitrogen distribution among vegetation and soil components, and understorey floristics suggest important considerations for management of plantations established on degraded tropical sites. Given that a considerable fraction of the carbon and nitrogen stores in the plantation system occur in aboveground vegetation, early harvest and removal of most or all of the tree crop (*Albizia*) would negate a significant percentage of the system carbon and nitrogen gains. Extensive tree harvests could also have a negative influence on understorey development by changing the understorey microclimate in ways that would inhibit secondary forest tree species recruitment. For example, increased light levels in the understorey would probably favor the growth of grasses, which in turn could suppress seed germination and/or early seedling growth of forest tree species. If early tree harvests are required for economic reasons, a more judicious approach may be to selectively harvest trees (rather than clear-cut) within the plantation system, so as to maintain a more or less continuous canopy and an understorey microclimate favorable to natural successional processes. Alternatively, plantation harvests could be delayed until understorey tree species assume a more significant structural role in the plantation canopy. Harvest of the plantation crop at this stage would presumably have less of a negative impact on understorey development.

The role of understorey forbs and grasses as short-term reservoirs for carbon and other elements, particularly nitrogen, is noteworthy. Although these components constitute a relatively minor fraction of the total biomass in the plantation system, the understorey flora appears to respond to increased nitrogen availability in the mineral soil by storing significantly greater concentrations of nitrogen in leaves and other plant structures. This phenomenon may help to reduce nutrient leaching losses and thus conserve nitrogen within the plantation system in living biomass and in slowly decomposing litter and soil organic matter. Earlier studies focusing on the role of understorey vegetation in nutrient cycling and understorey effects on nitrogen leaching rates in *Pinus* plantations (Kellman et al., 1987; Smethurst and Nambiar, 1989); provide some support for this hypothesis. Thus, management of plantations established on degraded sites should optimally aim at retaining understorey vegetation in order to maximize system nutrient gains and, of course, to foster biological diversity and development of mixed secondary forests which may eventually replace the monospecific plantation stand.

A similar case could be made for plantation management approaches that ensure the continued development of the forest floor. The forest floor is an important reservoir of organic carbon and nutrients, and helps to insulate the mineral soil surface, thereby moderating fluctuations in soil humidity. The forest floor also serves as a physical barrier that reduces the kinetic energy of incoming rainfall and throughfall, and thus its capacity to leach available nutrients from upper soil horizons. The forest floor may also play an important role in forest tree seed germination and seedling survival by providing favorable germination microhabitats and, perhaps, by precluding the growth of thick grass swards that may suppress seedling growth.

CONCLUSIONS

The results of the present study indicate that plantation monocultures established on degraded tropical sites can greatly accelerate processes of plant succession and rates of biomass and nutrient accretion in vegetation and soils. In comparison with adjacent control areas, 4.5-year-old *Albizia lebbek* plantation stands showed an 11-fold increase in aboveground plant biomass, a 7-fold increase in root and forest floor biomass, and marked differences in aboveground and belowground structure (vertical distribution of biomass and nutrients). Understorey vegetation was floristically different between treatments, particularly with respect to naturally regenerating secondary forest tree species, which were absent in the control. Nitrogen concentrations in plant tissues and forest floor biomass were generally much higher in the plantation system, as were soil organic carbon and soil nitrogen concentrations. Total system carbon and nitrogen stores were 1.90 and 1.64 times higher, respectively, in the plantation than in the control. These results suggest that with careful species selection and management practices based on an understanding of natural succession and nutrient cycling processes, forest plantations are a promising tool for tropical wasteland rehabilitation.

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