CHAPTER 15

Assisted Recovery of Degraded Tropical Lands: Plantation Forests and Ecosystem Stability

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ABSTRACT

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

Mineral soil (0 to 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). Standing crop mass of herbaceous plants, forest floor organic matter, and fine (<2 mm) roots averaged 160, 349, and 362 g/m^2 in the plantation plots and 420, 311, 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 understory 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 understory, but absent in control plots, suggesting an important role for such plantations in accelerating natural regeneration of native forest species on certain sites.

I. INTRODUCTION

Environmental degradation, though not a recent phenomenon in either temperate or tropical regions, has intensified in recent decades to the extent that it now poses a serious threat to the maintenance of biological diversity, agricultural productivity, and environmental stability in affected regions.

Numerous studies have demonstrated that plantations of native or exotic tree 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 (O'Connell, 1986; Gill et al., 1987; Montagnini and Sancho, 1990), moderation of soil pH, and improvement of soil nutrient status (Sanchez et al., 1985; Chakraborty and Chakraborty, 1989, Sharma and Gupta, 1989). The development of a plantation canopy can alter the understory 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; Pande et al., 1988; 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).

Albizia lebbek (L.) Benth. — a nitrogen-fixing, leguminous, multipurpose 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 fooder, tannins, gums, and traditional medicinal products (Parrotta, 1987). The present study, conducted at a degraded coastal pasture site in Puerto Rico, examines the cumulative effects of 4.5-year-old *A. lebbek* plantations on aboveground and belowground biomass and nutrient storage patterns and understory community structure.

II. MATERIALS AND METHODS

A. Site Description

The investigation was conducted at the University of Puerto Rico 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/year, and is moderately seasonal in distribution. Average daily temperatures ranges from 23.8°C in January to 29.4°C in August.

The soils are well drained, moderately alkaline (pH 7.9 to 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 that include cultivation and large-scale soil perturbations such as sand extraction and leveling. For approximately 2 to 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 (primarily Compositae, Leguminosae, and Euphorbiaceae); 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 four-month-old, *A. lebbek* seedlings were planted at spacings of 2 × 2 m, 1 × 1 m, and 0.5 × 0.5 m. Plot size varied depending on tree spacing: 1296, 324, and 81 m^2, for the low, intermediate and high-density treatments, respectively; and 200 m^2 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.

B. Field Measurements

In May 1989, 4.5 years after plantation establishment, aboveground and coarse root (>1-cm diameter) biomass of the tree crop *(A. lebbek)* was estimated from equations 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 sub-plot of each plantation plot (excluding a buffer zone comprised of the outer four rows of trees), 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. For each tree harvested, leaf, stem, and branch fractions were weighed in the field using appropriate spring scales. Subsamples of leaf biomass and randomly selected branch and stem segments from each size category were returned to the laboratory for dry mass conversion, wood-to-bark ratios, and nutrient analyses.

Floristic composition, aboveground biomass, litter (forest floor mass), and root biomass in control areas and in the plantation understory were measured in 1 × 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 located randomly. In the plantation plots, 21 quadrats were established — 4 in each of the low-density, 2 in each of the intermediate-density, and 1 in each of the high-density plots. Within plantation plots, quadrats were located randomly within a central 10 by 10 tree sub-plot to avoid possible edge effects.

Prior to harvest, all species occurring in each quadrat were identified and, for woody seedlings, height and basal diameters were recorded. All live plant material was harvested and separated by life form (grasses, vines and forbs, woody seedlings). Leaf and branch litter retained by a 1.0-mm sieve was collected from a central 0.5 × 0.5 m area within each quadrat. The mass of fine and small roots (<2 mm and 2–10 mm diameter, respectively) was estimated by harvesting all roots in a 30 × 30 cm pit dug from the center of each quadrat to a depth of 40 cm. All live and dead roots occurring in each 10-cm stratum were collected by hand (for larger roots) or by sieving with a 1-mm mesh.

A composite mineral soil sample comprising three 20-cm cores was taken within each quadrat using a 1.4-cm diameter tube sampler. Twenty additional 20-cm cores were taken for bulk density measurements using a 5.1-cm diameter tube sampler, ten cores each in the control and plantation plots.

C. Laboratory Analyses

All aboveground biomass, forest floor, and root samples were oven-dried at 65°C to constant weight. Samples of *A. lebbek* branch and stem components were separated into wood and bark fractions for determination of wood-to-bark ratios and for subsequent nutrient analyses.

Dried vegetation samples were ground in a Wiley mill, after which 1.5-mg subsamples wee analyzed for nitrogen and carbon content using a Carlo Erba elemental analyzer. Three to six randomly selected subsamples of each biomass component were combusted at 550°C for 4 hr in a muffle furnace to determine ash-free dry weights.

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 de-ionized water. Organic carbon was determined by the Walkley-Black method (Allison, 1965). Measurements of total Kjeldahl nitrogen were made using standard digestion and colormetric techniques (Tecator, 1986).

III. RESULTS AND DISCUSSION

A. 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, respectively, across all density treatments.

Table 1. Equations Used to Estimate *Albizia lebbek* Aboveground and Coarse Root Biomass in Plantation Plots

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

Note: Regressions based on 36 trees harvested from within plantation plots. Mean height of sample trees = 5.2 ± 0.4, mean basal diameter = 8.0 ± 0.8 (standard error [SE]); Y = oven-dry mass (kg); H = tree height (m); D = basal diameter (cm); Br/St: stems + branches.

Table 2. Plant Dry Mass (Mean ± SE) in *Albizia lebbek* Plantation Plots and Adjacent Control Area 4.5 Years after Plantation Establishment

Biomass category	Standing Biomass (g/m²)	
	Plantation[a]	Control[b]
Albizia lebbek		
Leaf	380 ± 110	0
Br/St <1 cm	220 ± 50	0
Br/St 1–2.5 cm	820 ± 210	0
Br/St >2.5 cm	3070 ± 470	0
Total *Albizia*	(4490 ± 840)	(0)
Understory vegetation		
Grasses	96 ± 27	312 ± 72
Vines/forbs	47 ± 20	108 ± 24
Woody seedlings	17 ± 7	0
Total understory	(160 ± 25)	(420 ± 61)
Total aboveground biomass	4660 ± 1430	420 ± 61
Below soil surface		
Roots		
Fine roots (<2 mm)	362 ± 32	105 ± 14
Small roots (0.2–1 cm)	246 ± 68	23 ± 11
Coarse roots (>1 cm)	2115 ± 648	0
Total roots	(2723 ± 729)	(129 ± 21)
Forest floor (litter)	349 ± 45	311 ± 61
Total belowground	3072 ± 723	440 ± 72
Total above- and belowground dry mass	7718 ± 2149	860 ± 124

[a] 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.
[b] n = 15 for all control plot mean values: based on 1 × 1 m quadrat data.

Aboveground dry mass in the plantation plots was estimated to be 4660 g/m² (Table 2). *Albizia* stems and branches (4110 g/m²) and leaves (380 g/m²) comprised 96.4% of the total. Understory vegetation (grasses, forbs and vines, woody seedlings) averaged 160 g/m². In contrast, aboveground biomass in the control averaged 420 g/m², significantly higher than plantation understory biomass. In the control, understory aboveground biomass as dominated by grasses (312 g/m²), which comprised an average of 74% of the total.

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 2723 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, Figures 1A and 1B). In the control areas, fine roots were not encountered below 30-cm depth, and 79% of the total fine root biomass occurred in the 0–10 m stratum. In the plantation plots, fine roots were encountered to a depth of 40 cm. 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 plantation crop *(Albizia)* in the former. The majority of fine roots and nearly all roots >0.2-cm diameter harvested from the plantation plots were identified as *Albizia*.

B. 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 4 grass species (Table 3). 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. Seedlings of secondary forest tree and shrub species, absent in the control, were abundant in the plantation plots, with a mean density of 1.14 seedlings per square meter for all species. The most common tree species found in the plantation understory were *Citharexylum fruticosum* (pasture fiddlewood), *Spathodea campanulata* (African tulip tree), and *Eugenia monticola* (black cherry).

Of the 11 vine species found in the plantation quadrats, only *Centrosema virginianum* was found in the control. Among forb species, a total of 16 species occurred in the plantation vs 12 species in the control. *Bidens alba* was the most common in both the plantation and control. In terms of biomass, vines constituted a relatively small fraction of the vine/forb category in both the plantation and control plots.

Striking differences between treatments were found in the distribution of grass species. *Brachiaria subquadripara*, the species occurring most frequently in the plantation quadrats, was absent in the control. Grass species occurring most frequently in the control — *Panicum maximum*, *Eustachys petraea*, and *Tricholaena repens* — were much less common in the plantation.

Several inter-related factors may account for the relative floristic richness of the plantation plots. Studies of succession in Amazonian forest ecosystems following various types of human disturbance (Uhl et al., 1982; Uhl, 1987; Nepstad et al., 1991) have suggested a number of barriers to natural regeneration of forest tree species on degraded sites, including low propagule availability, seed pre-

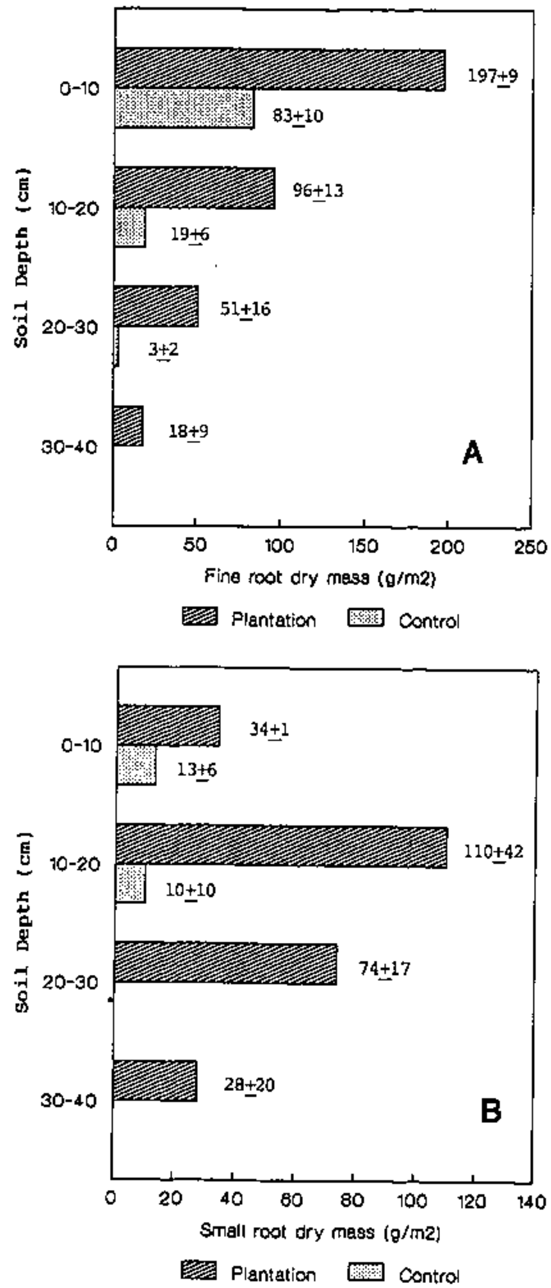

Figure 1. Root biomass and depth distribution in plantation and control plots. (A) Fine roots (<2 mm diameter). (B) Small roots (2–10 mm diameter). Bar values indicate mean dry mass ± SE.

Table 3. Plant Species Occurring in *Albizia lebbek* Planation Understory and Control Plots

Genus and species	Family	Frequency (% of quadrats) Plantation plots	Control plots
Trees/shrubs			
Schinus terebinthifolius Raddi	Anacardiaceae	5	0
Rauvolfia nitida Jacq.	Apocynaceae	5	0
Spathodea campanulata Beauv.	Bignoniaceae	14	0
Calophyllum brasiliense Camb.	Guttiferae	5	0
Albizia lebbek (L.) Benth.	Leguminosae (M)	5	0
Indigofera suffruticosa Miller	Leguminosae (P)	5	0
Lonchocarpus latifolius (Willd.) DC.	Leguminosae (P)	5	0
Murraya paniculata (L.) Jack	Rutaceae	14	0
Melicoccus bijugatus Jacq.	Sapindaceae	5	0
Citharexylum fruticosum L.	Verbenaceae	33	0
Lantana camara var. *aculeata* (L.) Mold.	Verbenaceae	5	0
Vines			
Centrosema pubescens Benth.	Compositae	33	0
Centrosema virginianum (L.) Benth.	Compositae	48	60
Melothria pendula L.	Cucurbitaceae	10	0
Momordica charantia L.	Cucurbitaceae	33	0
Galactia striata (Jacq.) Urban	Leguminosae (P)	5	0
Stylosanthes hamata (L.) Taub.	Leguminosae (P)	5	0
Jasminium fluminense Vell.	Oleaceae	10	0
Passiflora edulis Sims	Passifloraceae	14	0
Passiflora multiflora L.	Passifloraceae	5	0
Passiflora suberosa L.	Passifloraceae	10	0
Cissus verticiliata L.	Vitaceae	5	0
Forbs			
Cordia polycephala (Lam.) I.M. Johnst.	Boraginaceae	10	0
Commelina elegans HBK.	Commelinaceae	38	40
Bidens alba (L.) DC. var. *radiata* (Sch.-Bip.) Ballard	Compositae	86	80
Melanthera aspera (Jacq.) L.C.Rich. ex Spreng.	Compositae	5	0
Vernonia cinerea (L.) Less.	Compositae	10	0
Chamaesyce hirta (L.) Millsp.	Euphorbiaceae	5	20
Euphorbia heterophylla L.	Euphorbiaceae	19	0
Jatropa gossypifolia L.	Euphorbiaceae	0	7
Chamaecrista nictitans (L.) Moench. ssp. *nictitans*	Leguminosae (C)	14	20
Mimosa pudica L.	Leguminosae (M)	33	33
Crotalaria retusa L.	Leguminosae (P)	10	13
Desmodium incanum DC.	Leguminosae (P)	0	7
Desmodium tortuosum (Sw.) DC	Leguminosae (P)	19	13
Desmodium triflorum (L.) DC.	Leguminosae (P)	14	7
Tephrosia senna HBK.	Leguminosae (P)	10	33
Sida rhombifolia L.	Malvaceae	5	0
Spermacoce verticillata	Rubiaceae	5	15
Unidentified forb		5	0
Grasses			
Brachiaria subquadripara (Trin.) Hitch.	Graminae	67	0
Eustachys petraea (Sw.) Desv.	Graminae	33	53
Panicum maximum Jacq.	Graminae	14	67
Tricholaena repens (Willd.) Hitchc.	Graminae	14	53

Note: Data derived from 1 × 1 m quadrats.

dation, 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* (passion fruit) are commonly bird-dispersed. For large-seeded tree species such as *Calophyllum brasiliense*, bats are the likely dispersal agents. Presence in the plantation understory and absence in the control of tree species with wind-dispersed seeds (e.g., *Spathodea campanulata*) are likely due to 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 plantation 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 understory. Differences in the relative abundance of grass species in the control and plantation understory may be influenced by microclimatic variables or soil nutrients.

C. System Nutrient Distribution and Soil Fertility

Nitrogen concentrations in vegetation and soil compartments were markedly different between the plantation and control plots (Table 4). Among biomass components common to both plantation and control treatments (grasses, vines/forbs, fine roots, and forest floor), nitrogen concentrations in the plantation were 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 understory 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 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. 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 in soil organic carbon and rise in soil nitrogen may have been

Table 4. Nutrient Concentrations (Mean ± SE) in Plant Tissues and Soils in Experimental Plantation Plots and Control Areas

			% ash-free DW	
		n	Carbon	Nitrogen
Albizia lebbek				
Leaf		34	50.8 ± 0.5	4.15 + 0.11
Br/St <1 cm	- wood	7	45.1 + 0.1	0.96 ± 0.20
	- bark	8	46.0 ± 2.0	2.03 ± 0.26
Br/St 1–2.5 cm	- wood	7	46.2 ± 0.1	0.41 ± 0.03
	- bark	9	47.4 ± 0.6	2.38 ± 0.17
Br/St < 2.5 cm	- wood	24	45.9 ± 0.2	0.26 ± 0.03
	- bark	24	47.7 ± 0.3	1.97 ± 0.06
Understory vegetation				
Grasses	- plantation	12	45.4 ± 0.4	2.04 ± 0.10
	- control	12	46.2 ± 0.4	0.97 ± 0.08
Vines/Forbs	- plantation	12	48.6 ± 0.9	2.83 ± 0.11
	- control	12	44.1 ± 0.7	1.27 ± 0.13
Woody spp.	- plantation	8	43.2 ± 1.3	1.87 ± 0.17
Roots				
Fine roots	- plantation	20	53.3 ± 0.4	2.49 ± 0.11
	- control	15	53.6 ± 0.9	2.12 ± 0.13
Small roots (0.2–1 cm)		21	50.0 ± 0.9	1.91 ± 0.10
Coarse roots (>1 cm)		10	48.8 ± 1.2	1.60 ± 0.15
Soils				
Forest Floor	- plantation	12	57.6 ± 1.1	3.34 ± 0.15
	- control	12	54.6 ± 2.8	1.90 ± 0.11
Mineral soil	- plantation	21	1.70 ± 0.12	0.095 ± 0.006
(0–20 cm)	- control	15	1.44 ± 0.17	0.074 ± 0.010

related to the acceleration of organic matter decomposition following site preparation (disk harrowing) prior to plantation establishment. 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 the plantation crop *(Albizia)* and its understory 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 similar to pre-plantation data. Mean soil bulk density was slightly, though not significantly, higher in the control (1.065 g/cm^3) than in the plantation (1.041 g/m^3).

System carbon and nitrogen storage patterns were markedly different between plantation and control plots, reflecting treatment differences and vegetation dry mass and differences in carbon and nitrogen concentrations among vegetation

Table 5. Estimated Carbon and Nitrogen Standing Stocks in *Albizia lebbek* Plantation Plots and Adjacent Control Area 4.5 Years after Plantation Establishment

	Total element store (g/m²)			
	Plantation		Control	
	C	N	C	N
Aboveground biomass				
Albizia lebbek				
Leaf	181	14.8	0	0
Br/St <1 cm[a]	96	2.9	0	0
Br/St 1–2.5 cm	365	6.8	0	0
Br/St >2.5 cm	1406	16.3	0	0
Total *Albizia*	(2048)	(40.8)	(0)	(0)
Understory vegetation				
Grasses	39	1.8	128	2.7
Vines/forbs	20	1.2	42	1.2
Woody seedlings	7	0.3	0	0
Total understory	(66)	(3.3)	(170)	(3.9)
Total aboveground	(2114)	(44.1)	(170)	(3.9)
Belowground biomass and soil				
Roots				
Fine roots (<2 mm)	146	6.8	43	1.7
Small roots (0.2–1 cm)	108	4.1	11	0.4
Coarse roots (>1 cm)	445	14.6	0	0
Total roots	(700)	(25.6)	(54)	(2.1)
Forest Floor	143	8.3	121	4.2
Mineral soil (0–20 cm)	3539	197.8	3067	157.6
Total belowground	(4382)	(231.7)	(3242)	(163.9)
System total	6496	275.8	3412	167.8

[a] For branch and stem components, total nutrient content estimated as the total biomass for that component (wood + bark) times the weighted average concentration of carbon or nitrogen concentration. Bark comprised an average of 41.0, 23.6, and 16.4% of the total dry mass (DM) for the Br/St <1 cm, Br/St 1–2.5 cm, and Br/St >2.5-cm size classes, respectively.

and soil components (Table 5). Carbon stores in the plantation were 90% greater than in the control (6.496 vs 3.412 kg C/m²). Aboveground *Albizia* biomass accounted for approximately 66% (2.05 kg C/m²) of the difference between plantation and control carbon stores. Differences in belowground carbon stores between treatments were also great (4.382 kg C/m² in the plantation, 3.242 kg C/m² in the control).

Similar patterns were found with respect to total nitrogen stores. Relative to the control, plantation nitrogen stores were approximately 64% higher (275.8 vs 167.8 g N/m²). Aboveground nitrogen stores were more than 11 times greater in the plantation than in the control (44.1 vs 3.9 g N/m²). Mineral soil nitrogen stores (157.6 g N/m²) comprised 96% of the belowground total in the control, with roots (2.1 g N/m²) and forest floor biomass (4.2 g N/m²) comprising the remainder. In the plantation, mineral soil nitrogen (197.8 g N/m²) 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 accumulated approximately 3.08 kg C/m² and 108 g N/m² 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. 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. Extrapolating 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.

Rates of system nitrogen accumulation in the present study (24 g/m^2/year) 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). The rapid rate of nitrogen accumulation in the plantation relative to the control strongly suggests the importance of biological nitrogen fixation in the plantation system and its role in ecosystem rehabilitation at this site.

D. Rehabilitation Processes and Management Implications

The observed patterns of biomass production, carbon and nitrogen distribution among vegetation and soil components, and understory floristics suggest important considerations for management of plantations established on degraded tropical sites. Given that a large 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 would negate a significant percentage of the system carbon and nitrogen gains. Extensive tree harvests could also have a negative influence on understory development by changing the understory microclimate in ways that would inhibit secondary forest tree species recruitment. For example, increased light levels in the understory 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 understory microclimate favorable to natural successional processes. Alternatively, plantation harvests could be delayed until understory tree species assume a more significant structural role in the plantation canopy.

The role of understory forbs and grasses as short-term reservoirs for carbon and, particularly, nitrogen is noteworthy. Although these components constitute a relatively minor fraction of the total biomass in the plantation system, the understory 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 understory vegetation in nutrient cycling and understory 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 understory 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 otherwise suppress seedling growth.

ACKNOWLEDGMENTS

I thank Alain Henri Liogier of the University of Puerto Rico Botanical Garden and Carlos Rivera of the Institute of Tropical Forestry (U.S. Department of Agriculture — Forest Service) for their help in identifying plant specimens. This work was conducted in cooperation with the Center for Energy and Environment Research, University of Puerto Rico, Rio Piedras.

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