6. Secondary forest regeneration on degraded tropical lands

The role of plantations as "foster ecosystems"

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Abstract. Forest plantations established on degraded sites can accelerate natural succession through their effects on vegetation structure, microclimate, and soils. Spatial and temporal patterns of secondary forest species regeneration were studied in permanent quadrats in *Albizia lebbek* plantation plots and control areas at a degraded coastal pasture in Puerto Rico. Approximately 6.7 years after plantation establishment, a total of 22 tree and shrub species were found in the plantation plots, compared with only one species (*Albizia lebbek*) found in the control plots. The majority of tree species in the plantation have seeds that are dispersed by either birds or bats, suggesting that the plantation canopy plays a key role in the regeneration process by providing roosting habitat for seed-dispersing animals. Spatial variations in plantation understory seedling populations were found to be associated with both distance from probable parent trees and understory light intensity. These results indicate profound differences between the plantation and adjacent control plots with respect to their provision of regeneration habitat for secondary forest species, and suggest several factors that should be considered in the design of "foster ecosystems" for the rehabilitation of severely degraded tropical forests.

Introduction

The rehabilitation of damaged tropical forests is a major challenge facing ecologists, foresters, and those who depend on productive and diverse forest ecosystems for their sustenance and livelihood. The scale and severity of forest damage, as well as the difficulties associated with their rehabilitation, vary greatly from site to site, and are a function of initial forest structure and species composition, soils, climate, complexity, and resilience of underlying ecosystem processes such as energy flows and biogeochemical cycling, history of disturbance, and the persistence and intensity of ecosystem stresses which inhibit or slow natural successional processes (Lugo 1988).

Severely degraded forest ecosystems, such as those occurring in mining areas throughout the tropics, *Imperata* grasslands of Southeast Asia, and degraded or abandoned pastures in Eastern Amazonia, sub-Saharan Africa, and many parts of India, require special attention if they are to quickly return to productivity. Severely degraded lands are typically characterized by eroded or nutrient-deficient soils, hydrologic instability, reduced primary productivity and low biological diversity. Persistent physical, chemical, and biological barriers often prevent natural succession processes from operating on a time scale compatible with short- and medium-term human needs (Uhl et al. 1982, 1988; Uhl 1987; Nepstad et al. 1991). These barriers to natural forest regeneration may include one or more of the following: low propagule availability (seeds, root stocks), seed predation, non-availability of suitable microhabitats for plant establishment, low soil nutrient availability, absence of obligate or facultative fungal or bacterial root symbionts, seedling predation, seasonal drought, root competition with old field vegetation (particularly grasses), and fire.

An appropriate goal of forest ecosystem rehabilitation is to facilitate, accelerate, and direct 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

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within the recovering ecosystem. Forest plantations, using carefully selected tree and shrub species, can play an important role in tropical forest rehabilitation (Lovejoy 1985; Lugo 1988). Numerous studies have demonstrated that plantations of native and exotic species adapted to the harsh conditions of degraded sites can reverse degradation processes by stabilizing soils, increasing soil organic matter through enhancement of above- and below-ground litter production and turnover (Lowry et al. 1988; Montagnini and Sancho 1990), moderation of soil pH, and improvement of soil nutrient status (Sanchez et al. 1985; Chakraborty and Chakraborty 1989; Parrotta 1992).

Through their localized effects on microclimatic and biotic conditions, plantations can facilitate recruitment, survival, and growth of native forest species in the understory, thus acting as "foster ecosystems" (Lugo 1988) for species-rich secondary forests. *Albizia lebbek*, a nitrogen-fixing, leguminous tree species chosen for this study, exhibits a number of characteristics that make it a good candidate for restoration of degraded tropical lands. Native to South Asia and naturalized in many parts of the Caribbean, including Puerto Rico, 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 1987).

This paper presents the results of a study of secondary forest regeneration within *Albizia lebbek* plantation plots and control areas at a degraded coastal site in Puerto Rico. Patterns of recruitment, survival, and growth of woody seedlings are evaluated over a two-year period between 4.5 and 6.7 years after plantation establishment. The factors affecting spatial distribution of secondary forest recruits, and their implications for the design and management of foster ecosystems, are discussed.

Site description and history

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, with two to five months per year in which rainfall is less than 100 mm. Average daily temperatures range from 23.8 °C in January to 29.4 °C in August. Winds at this site are predominantly northeasterly to southeasterly throughout the year.

The soils are well-drained, moderately alkaline (pH 7.9–8.4), calcareous sands of marine origin (isohypothermic Typic Troposamments). Surface soil organic matter is highly variable within the experimental site (0.5–2.5%) and soil nitrogen (<0.1%) is low (Parrotta 1992). 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 levelling. 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* and *Tricholaena repens*, and a wide variety of forbs, primarily Compositae, Leguminosae, and Euphorbiaceae; woody plants were absent. A wooded pasture with a much less severe disturbance history, comprised of approximately 20 secondary forest tree species, borders the experimental area to the south and east (Fig. 1). Urban areas border both the northern and western site boundaries.

Methods

Plantation establishment

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 *Albizia lebbek* seedlings were planted at spacings of 2 × 2-m, 1 × 1-m, and 0.5 × 0.5-m. Plot size varied depending

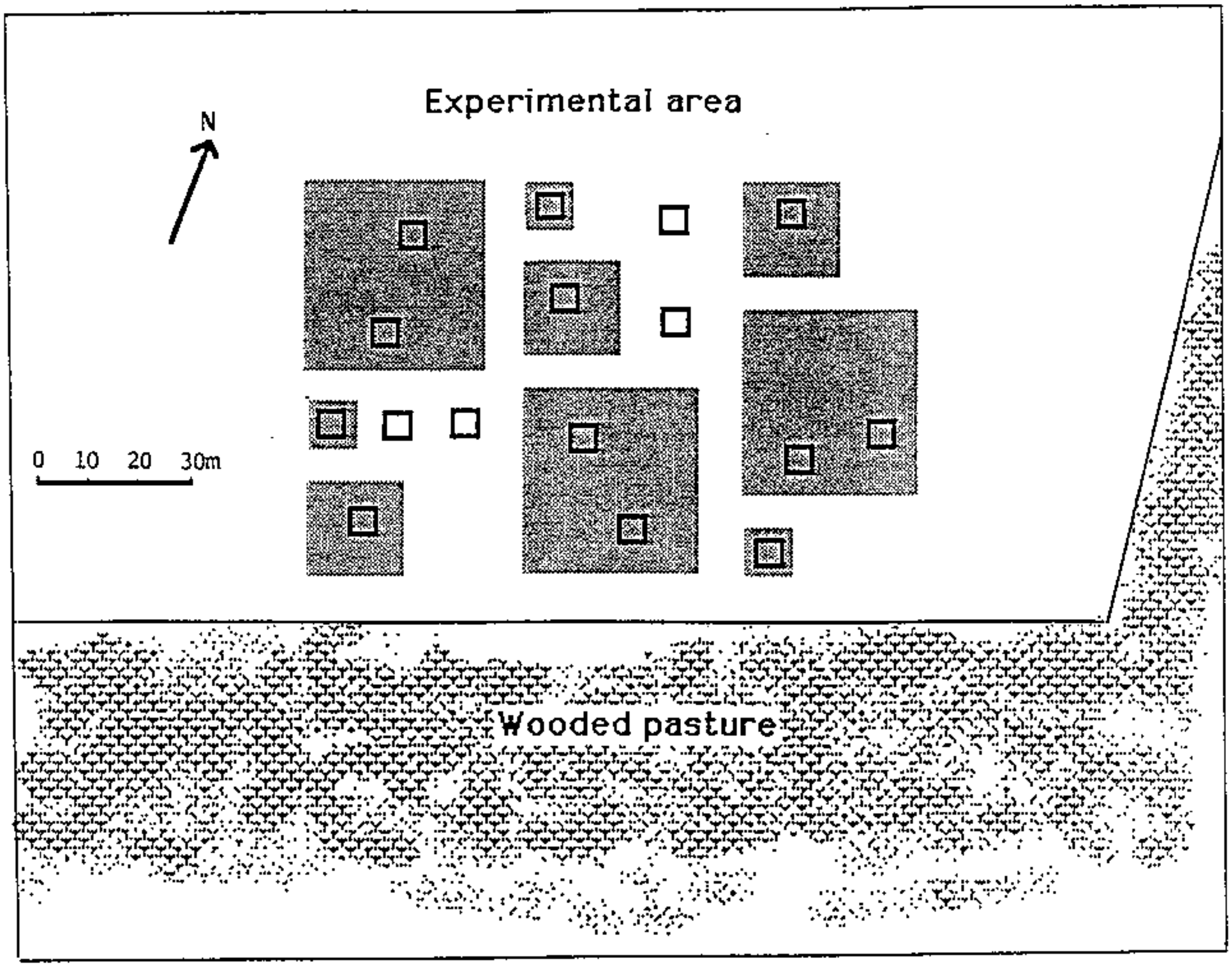

Fig. 1. Experimental site showing locations of permanent quadrats within *Albizia lebbek* plantation plots (shaded squares) and control plots (unshaded).

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 for the control plots. After planting, the site was protected from grazing and fire for the duration of the study. Approximately every two months during the first year of the experiment, plantation plots were manually weeded. Plantation plots were neither irrigated nor fertilized. Within one year of plantation establishment, vegetation within the control areas was structurally and floristically similar to that which occurred on the site prior to site preparation, and was dominated by grasses and forbs.

In May 1989, biomass, vegetation and soil macronutrient stores, and understory floristics were evaluated in both the plantation and control plots (Parrotta 1992). At this time, plantation stand parameters in the low, intermediate, and high density treatments, respectively, were as follows — mean tree height: 5.0, 4.2, and 2.6 m; total basal area: 17, 25, and 44 m^2 ha^{-1}; total above-ground tree biomass: 32, 42, and 61 Mg ha^{-1}. Total understory biomass, dominated by grasses, averaged 185, 92, and 203 g m^{-2} in the low, intermediate, and high density plantation treatments, and 420 g m^{-2} in the control plots. Seedlings of secondary forest tree species, absent in the control plots, occurred in the plantation plots at an average density of 1.14 m^{-2}. No consistent differences among plantation density treatments were noted with respect to understory floristics, understory biomass, or seedling density.

Study design

In May 1990, a total of twelve 16-m^2 permanent quadrats were established in the plantation plots: two in each of the largest three plots, and one in each of the remaining six plots. Quadrats were located randomly within the central zone of each plot (excluding the 4 outer tree rows). An additional four quadrats were located in the control plots (Fig. 1). Within each quadrat, all woody seedlings taller than 5 cm were identified, mapped, and tagged. Basal diameters and total heights were recorded. At four-month intervals thereafter, until August 1991, all seedlings present earlier were measured, mortality noted, and new recruits identified, measured, mapped and tagged.

Over several days in July and August 1990, understory light intensity was measured between 8:00 and 13:00 hours using a portable light meter at numerous (10–20) points within each quadrat at a height of 1.0 m in both the plantation and control plots. As the vegetation height within the control plots averaged 60 to 90 cm, these values represented open light conditions. Light intensity readings were averaged over all measurement dates to yield a mean value for each quadrat.

Seed dispersal mechanisms and minimum dispersal distances were evaluated for all woody species represented in the permanent quadrats. Likely dispersal mechanisms (e.g. wind, birds, bats) were based on an evaluation of seed characters and a review of the literature. Minimal dispersal distances, estimated for all species in each quadrat, were based on a survey of reproductively mature individuals found in the adjacent wooded pasture or elsewhere within a radius of 200 m from the study site.

Results and discussion

Species diversity, recruitment, and population dynamics

Throughout the study period, dramatic differences were observed between the *Albizia* plantation and control plots with respect to both population densities and diversity of secondary forest species. In the control quadrats, the only species represented in the seedling flora was *Albizia lebbek*, which occurred at an average density of 0.03 to 0.11 individuals per m^2 across all measurement dates, with no individuals larger than 80 cm in height. In contrast, the plantation understory quadrats included seedlings of a total of 21 to 23 tree and shrub species during the period from May 1990 to August 1991 (corresponding to plantation ages of 5.4 and 6.7 years). During this period, seedling densities increased from 1.93 to 2.82 individuals per m^2, of which 17 to 25% were *Albizia lebbek* and 35 to 41% were the successional forest species *Citharexylum fruticosum* (Fig. 2a). Also during this period, the mean number of secondary forest species represented in the seedling flora of the twelve permanent quadrats increased from (all values are mean $\pm$ SE) 6.5 ± 0.9 to 8.4 ± 0.6 per 16-m^2 quadrat. These data suggest that while the total number of tree and shrub species in the plantation remained more or less constant, the spatial distributions of these species were becoming more even over time.

Differences among plantation density treatments were noted with respect to understory seedling density. At 6.7 years, mean seedling densities for secondary forest species were 1.72 ± 0.41, 2.08 ± 0.96 and 2.77 ± 0.90 individuals per m^2 in the low, intermediate, and high density treatments, respectively. An opposite trend was noted for *Albizia lebbek* seedlings which occurred at densities of 0.81 ± 0.22, 0.67 ± 0.23, and 0.50 ± 0.38 individuals per m^2 within the three plantation density treatments. However, as these differences were not statistically significant, data from all plantation understory quadrats were pooled for subsequent analysis. Density, mean seedling basal diameters and heights, and importance values (Curtis 1959) for each of the species found in the plantation and control quadrats at the end of the study period are given in Table 1.

At 6.7 years of age, the plantation understory seedling basal area was 5.45 cm^2 per m^2. The corresponding value for the control plots was 0.026 cm^2 per m^2. As indicated in Fig. 2b, the dominant tree species in the plantation understory, *Citharexylum fruticosum*, accounted for 75 to 77% of the total seedling basal area. While

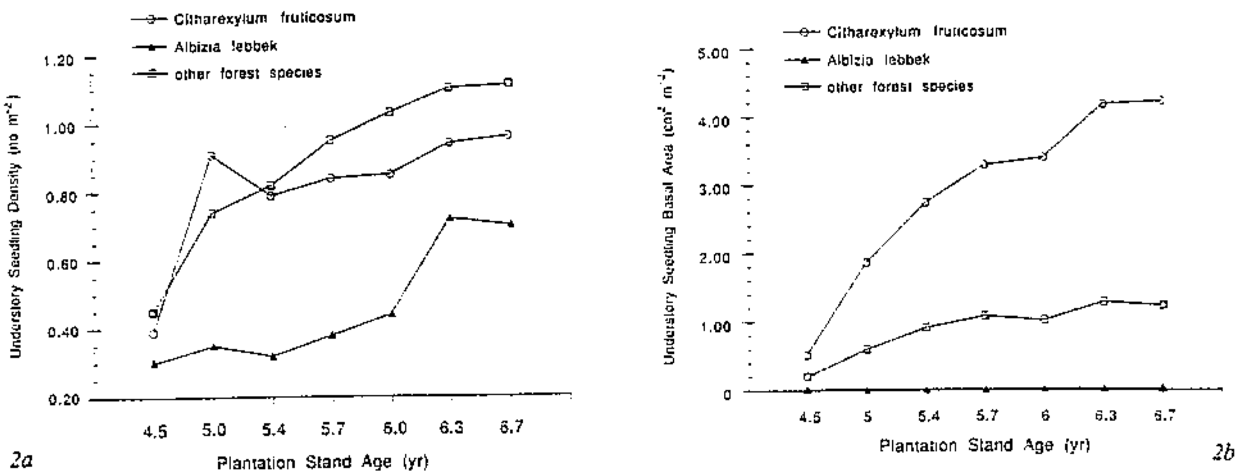

Fig. 2. Tree and shrub seedling/sapling population trends in plantation understory 4.5 to 6.7 years after plantation establishment. Data at 4.5 and 5 years derived from surveys involving 46 m^2 and 54 m^2 total quadrat area; 5.4 to 6.7 year data derived from permanent quadrat surveys (192 m^2). a. Understory seedling density. b. Understory seedling basal area.

Table 1. Understory seedling population characteristics and importance values (Curtis 1959), for tree species occurring in plantation and control quadrats in August 1991, 6.7 years after plantation establishment. Values following means indicate standard errors

Species	Seedling density (No. m^{-2})	Mean basal diameter (cm)	Mean seedling height (m)	Importance Value (I.V.)
Plantation				
Citharexylum fruticosum	0.974	1.76 ± 0.12	1.72 ± 0.12	124.0
Albizia lebbek	0.724	0.17 ± 0.01	0.17 ± 0.01	36.5
Cordia polycephala	0.146	1.11 ± 0.17	1.48 ± 0.25	20.5
Rauvolfia nitida	0.161	1.26 ± 0.15	1.23 ± 0.15	19.1
Lonchocarpus latifolius	0.234	0.79 ± 0.08	0.80 ± 0.10	15.4
Spathodea campanulata	0.089	1.19 ± 0.20	0.88 ± 0.27	14.6
Bourreria succulenta	0.115	0.92 ± 0.20	1.04 ± 0.24	12.9
Eugenia monticola	0.099	0.36 ± 0.04	0.33 ± 0.04	11.7
Schinus terebinthifolius	0.053	0.63 ± 0.19	0.87 ± 0.34	8.6
Roystonea borinquena	0.057	0.52 ± 0.12	0.37 ± 0.07	8.2
Calophyllum brasiliense	0.047	0.59 ± 0.15	0.49 ± 0.14	7.8
Bursera simaruba	0.036	0.81 ± 0.14	1.06 ± 0.28	7.1
Andira inermis	0.026	0.50 ± 0.05	0.34 ± 0.02	3.2
Psidium guajava	0.010	0.70 ± 0.10	0.85 ± 0.10	2.5
Trichilia hirta	0.005	0.50	0.16	1.4
Terminalia catappa	0.005	1.50	0.80	1.4
Albizia procera	0.005	1.10	1.25	1.3
Unidentified species (5)	0.036	0.79 ± 0.35	0.59 ± 0.26	3.8
Pasture control				
Albizia lebbek	0.109	0.43 ± 0.14	0.31 ± 0.10	

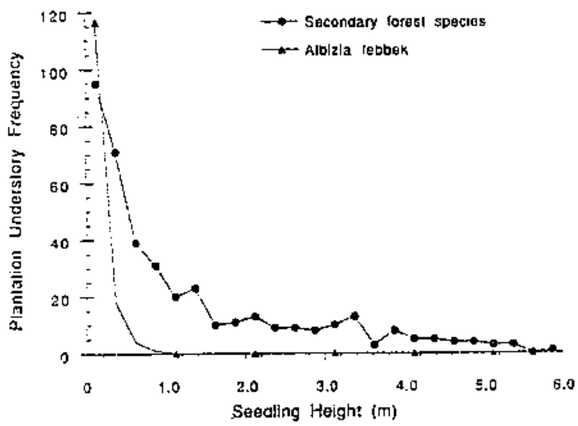

Fig. 3. Height distribution for secondary forest species and *Albizia lebbek* in plantation understory quadrats 6.7 yrs after plantation establishment. Total quadrat area: 192 m^2.

seedlings of *Albizia lebbek* were common within the plantation, they comprised less than 2% of the total seedling basal area throughout the study period. In contrast to the secondary forest species, which exhibited a fairly broad seedling height distribution, the population structure of *Albizia lebbek* understory seedlings was sharply skewed toward the smallest height classes (Fig. 3). Despite abundant seed production by the plantation crop since the second year after plantation establishment, the understory *Albizia* seedling population was dominated by small and in most cases very young individuals. Only 17% of the *Albizia lebbek* seedlings in the plantation understory quadrats at 6.7 years were taller than 25 cm. In contrast, 77% of *Citharexylum fruticosum* seedlings and 76% of seedlings of all other secondary forest species exceeded this height.

Seedling mortality patterns also suggest that relative to the secondary forest species, *Albizia lebbek* does not survive well in the plantation understory. Between 5.4 and 6.7 years a total of 264 seedlings were recruited into the permanent quadrats (192 m^2 total area), including 138 *Albizia lebbek* and 44 *Citharexylum fruticosum.* During this period, 96 seedlings died, including 65 *Albizia* and 10 *Citharexylum*. Thus, seedling mortality rates during this 1.3-yr period were 36% overall; 47% for *Albizia*, 23% for *Citharexylum*, and 26% of all other secondary forest species.

Table 2. Dispersal characteristics of secondary forest species occurring in *Albizia lebbek* plantation plots

Species	Importance value rank	Distance* from seed source (m)	Diaspore dispersal mechanism
Citharexylum fruticosum	1	>50	Birds
Albizia lebbek	2	0	Wind
Cordia polycephala	3	>30	Birds
Rauvolfia nitida	4	>90	Birds
Lonchocarpus latifolius	5	>20	Wind
Spathodea campanulata	6	>35	Wind
Bourreria succulenta	7	>50	Birds
Eugenia monticola	8	>200?	Birds
Schinus terebinthifolius	9	>200?	Birds
Roystonea borinquena	10	>20	Birds
Calophyllum brasiliense	11	>150	Bats
Bursera simaruba	12	>50	Birds/ mammals
Andira inermis	13	>200?	Mammals
Psidium guajava	15	>200?	Birds
Trichilia hirta	16	>200?	Birds
Terminalia catappa	17	>65	Bats
Albizia procera	18	>100	Wind
Unidentified species (5)	14,19–22	?	?

* Distance to nearest reproductively mature individual for each species located within a 200-m radius of the plantation site. "?" Indicates that no such individuals were found within this distance of the site.

Seed dispersal and the role of animals as successional catalysts

The absence of secondary forest species in the control plots, in marked contrast to the plantation, strongly suggests that pre-plantation soil seed banks at this site have played only a minor role in the observed patterns of understory seedling regeneration and that the forest succession process has been dominated by post-plantation seed introductions. Of the secondary forest species found in the plantation understory at 6.7 years, most have seeds that are typically dispersed by birds (Table 2). These species, such as *Citharexylum fruticosum, Cordia polycephala, Rauvolfia nitida, Roystonea borinquena,* and *Psidium guajava* (guava) are small-seeded species that produce fleshy fruits consumed by birds. At least two species, *Calophyllum brasiliense* and *Terminalia catappa*, produce large-

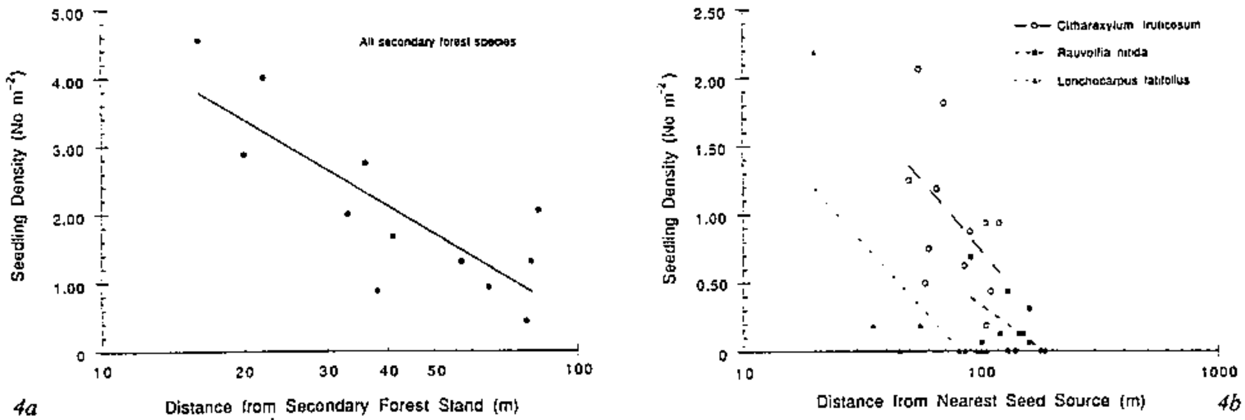

Fig. 4. Relation between seedling density in plantation understory quadrats at 6.7 yrs and distance from nearest potential seed sources. a. All secondary forest tree and shrub species, excluding *A. lebbek* ($r^2 = 0.66$; $P < 0.01$). b. *Citharexylum fruticosum* ($r^2 = 0.25$; $P < 0.10$), *Rauvolfia nitida* ($r^2 = 0.31$; $P < 0.10$), and *Lonchocarpus latifolius* ($r^2 = 0.54$; $P < 0.01$). Correlation coefficients and significance levels are for regressions for the general form: $y = a - b * \log_{10} x$.

seeded fruits that are most commonly dispersed by bats. Only three species, *Lonchocarpus latifolius*, *Spathodea campanulata*, and *Albizia procera*, can be characterized as wind-dispersed species. Thus, animal dispersal appears to be the dominant mechanism of seed input to the plantation system.

Based on a comparison of plantation understory seedling data and a survey of reproductively mature trees found within a 200 m radius of the plantation site, the minimum distances over which the seeds of these species were transported was estimated (Table 2). Seeds of most of the more common species appear to have been transported by animals or wind relatively short distances (<100 m). A few, notably *Eugenia monticola*, *Schinus terebinthifolius*, *Andira inermis*, *Psidium guajava* and *Trichilia hirta*, all bird- or mammal-dispersed species, were carried much further, since these species were not represented in the local flora within 200 m of the plantation site. These data suggest that the plantation is serving an important function in the process of secondary forest regeneration, or succession, by providing roosting and in some cases nesting habitat for frugivorous birds and bats.

Early in the study, it was noted that seedling densities and species distributions showed considerable variation with location within the plantation system. Comparing seedling populations among quadrats located in plantation plots (at 6.7 years), a significant negative correlation ($P < 0.01$) was observed between tree seedling density (for all species) and distance from the secondary forest stand adjacent to the experimental area (Fig. 4a). This relationship between minimum seed dispersal distance and quadrat seedling density appeared to be less pronounced when individual species were evaluated (Fig. 4b). Nonetheless, these trends do suggest that for species whose seeds are dispersed by either wind or animals, proximity to seed sources may be a very important factor controlling the rate of secondary forest species colonization of the plantation plots. It should be noted that within the plantations, the larger individuals of a few species, notably *Citharexylum fruticosum* and *Cordia polycephala*, had begun to produce flowers and mature fruits when the plantations were approximately four years old.

As a larger number of individuals and species within the plantation system become reproductively mature, it could be expected that the relative importance of external seed inputs into the plantation system would diminish over time, although external seed sources would continue to be important for increasing floristic biodiversity.

Understory light intensity, microhabitat structure and competition

A second factor, independent of seed source proximity, which appears to play a role in con-

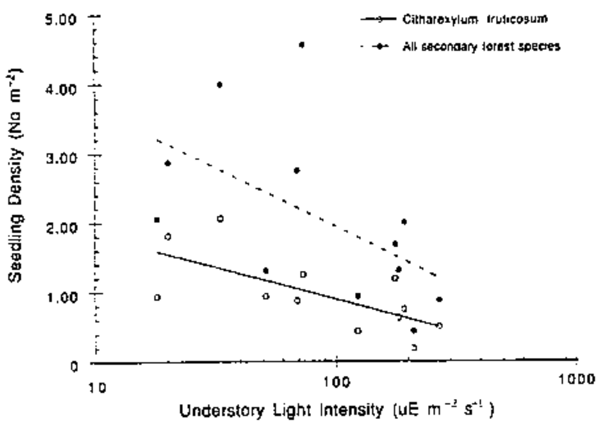

Fig. 5. Relation between seedling density and light intensity in plantation understory quadrats at 6.7 yrs. All secondary forest tree and shrub species, excluding *A. lebbek* ($r^2 = 0.31$; $P < 0.10$) and *Citharexylum fruticosum* ($r^2 = 0.48$; $P < 0.05$). Correlation coefficients and significance levels are for regressions for the general form: $y = a - b * \log_{10} x$.

trolling understory seedling density is light intensity. Understory light intensities, measured in July and August 1990, ranged from 18 to 269 μE m^{-2} s^{-1} (mean $\pm$ SE 118 ± 24) in the plantation quadrats, or 2 to 29% of the light intensities in the control plots, which averaged 924 μE m^{-2} s^{-1}. The wide range of understory light conditions in the plantation plots, highly correlated with canopy leaf area index (unpublished data), are the result of variable growth rates of the plantation crop and mortality of some larger trees caused by the vascular wilt *Fusarium solani* (Parrotta 1990). Following rapid initial growth of the planted *Albizia lebbek*, culminating in maximum mean annual wood increments between two and five years across all density treatments, canopy structure has become progressively less uniform within the plantation plots, with a general trend toward greater light penetration to the forest floor. A significant inverse relationship between seedling density and understory light intensity was found for all secondary forest species (excluding *Albizia lebbek*) and for *Citharexylum fruticosum* (Fig. 5).

It is unlikely that light intensity is exerting any direct control over seed germination or subsequent seedling survival in the plantation system. Most of the secondary forest species considered here are either pioneer species or otherwise capable of natural regeneration under conditions of full sunlight or light shade. Several inter-related factors could help to explain the apparent negative relationship between understory light intensity and seedling population density. Quadrats characterized by higher light levels tended to occur on sites with coarser sands relatively low in organic matter, and also tended to be more dominated by grasses than were quadrats with lower light levels. Thus the relative paucity of seedlings in the more open plantation quadrats could be the result of some combination of the following factors: (a) increased root competition with other understory floristic components, principally grasses; (b) less favorable soil moisture conditions affected by soil texture and soil organic matter; and (c) lower soil nutrient availability.

These same factors may also help to account for the dramatic differences observed between the plantation and control plots with respect to secondary forest regeneration, or rates of forest succession. Overall differences in light intensity, graminoid dominance, and soil properties between the degraded pasture control plots and the plantation understory, and the effects on seedling populations of microsite differences observed with regard to these factors among plantation quadrats, support this hypothesis. The relative importance of these factors, and the importance of differential seed input rates into plantation and control plots, is unclear and would require further study.

Implications for the design and management of "foster ecosystems"

The results of this study suggest that forest plantations established on degraded tropical lands can serve three important roles — (1) production of wood and other forest commodities, (2) soil improvement (Parrotta 1992), and (3) acceleration of secondary forest succession. The degree to which plantations realize these objectives is influenced by several factors, among the most important being species selection, plantation design, and management practices.

The choice of plantation species can influence both the rate and trajectory of rehabilitation processes. Candidate species may differ greatly in their capacity to resist or survive fire, drought, and other stresses, to stabilize soils, increase organic matter and available soil nutrients (Gill et al. 1987; Sharma and Gupta 1989; Lugo et al. 1990; Wang et al. 1991); and facilitate understory development (Sommariba 1988; Pande et al. 1988). These differences relate to their relative susceptibility to pests and diseases, patterns of above-ground and root biomass accumulation (Jonsson et al. 1988; Parrotta 1989; Lugo et al. 1990), nutrient utilization and allocation (Jorgensen and Wells 1986; Wang et al. 1991), litter production and fine root turnover, 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 selective strains of *Rhizobium* or *Frankia* can have a dramatic effect on soil fertility through their production of readily decomposible, nutrient-rich litter and turnover of fine roots and nodules (Bernhard-Reversat 1988; Montagnini and Sancho 1990). In the case of planted exotic species, poor natural regeneration, as observed in *Albizia lebbek* in the present study, can be viewed as a positive trait if one of the goals of rehabilitation is the facilitation of secondary forest succession.

Plantation design considerations which may influence rates of forest species colonization include the location of planted forests in relation to primary and secondary forest stands, and plantation density. Proximity to seed-bearing trees and, for native forest species with animal dispersed seeds, the habitat requirements of frugivorous birds, bats, and other seed dispersers, appear to be key factors influencing development of floristic diversity in plantations.

Regardless of initial tree planting density, the recruitment of secondary forest species appears to depend on the maintenance of sufficient canopy cover to ease understory seedling competition with grasses through shading and to provide sufficient habitat diversity for birds and other seed dispersal agents. Plantation harvests should be designed to ensure at least partial canopy closure until the secondary forest species assume a more dominant structural role within the plantation system.

The influence of natural forest proximity on seed recruitment into plantations established on severely degraded sites poses a special problem for the restoration of secondary forests over large areas. On such sites, the establishment of continuous plantation forest cover would not be an economically viable option in most instances, since forest yields would most likely be relatively low given the initial productivity constraints. Thus, more creative strategies that take advantage of natural forest succession processes may be required.

One such approach could be the creation of planted forest "archipelagos" extending into the heart of the area to be rehabilitated from the edges of existing forests. In such a system, it is hypothesized, secondary forest species colonization would be most rapid in plantation "islands" closest to the edges of the natural forest and would proceed gradually toward areas further removed from seed sources. Over time, these forested islands might be expected to enlarge as secondary forest species colonize the edges of planted forest stands, and eventually merge with neighboring islands. Similarly, planted forest strips or corridors, again extending away from the edges of natural forest stands, could be used as a lower-cost alternative to continuous plantations over large areas.

Implicit in such a model for large-scale restoration of forest cover on severely degraded sites is an understanding of the life history requirements of species which one hopes to see established in the planted foster ecosystems. Of particular importance is an understanding of seed ecology, including dispersal characteristics, and microhabitat requirements for germination and seedling development. For complex tropical forests, our knowledge in these areas is fragmentary at best. However, by focusing on the ecology of better known native, early successional species, the initial species composition, size and spatial arrangement of such islands or corridors could, in theory, be designed so as to facilitate their rapid, early colonization, and catalyze forest succession processes at the lowest possible cost. For example, fruit-bearing species likely to attract birds, bats or other animals known to be key dispersal agents for desired secondary forest species, could be included in the plantations.

The inclusion of native forest surface soils in the potting mix of containerized seedlings prior to outplanting could facilitate the development of soil faunal and microfloral diversity. This in turn could improve prospects for successful colonization of secondary forest species and re-establishment of complex community interactions and ecological processes on sites which previously had been biologically impoverished.

While there are not universally applicable techniques for tropical forest rehabilitation and restoration, the use of planted forests as foster ecosystems to facilitate or catalyze natural forest succession, may be one important tool for rehabilitating highly degraded sites. However, the success of this approach would appear to be highly dependent on several factors relating to species selection, plantation density, location with reference to seed sources, availability of dispersal agents, and management approaches. The synthesis of ecological and silvicultural knowledge can be of great value in this process by helping us to identify the key barriers to natural forest succession characteristic of specific degraded sites and to intervene constructively to bypass these constraints.

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