Forest Regeneration in a Chronosequence of Tropical Abandoned Pastures: Implications for Restoration Ecology

T. Mitchell Aide[1]
Jess K. Zimmerman[2]
John B. Pascarella[1,3]
Luis Rivera[4]
Humfredo Marcano-Vega[1]

Abstract

During the mid-1900s, most of the island of Puerto Rico was deforested, but a shift in the economy from agriculture to small industry beginning in the 1950s resulted in the abandonment of agricultural lands and recovery of secondary forest. This unique history provides an excellent opportunity to study secondary forest succession and suggest strategies for tropical forest restoration. To determine the pattern of secondary succession, we describe the woody vegetation in 71 abandoned pastures and forest sites in four regions of Puerto Rico. The density, basal area, aboveground biomass, and species richness of the secondary forest sites were similar to those of the old growth forest sites (>80 yr) after approximately 40 years. The dominant species that colonized recently abandoned pastures occurred over a broad elevational range and are widespread in the neotropics. The species richness of Puerto Rican secondary forests recovered rapidly, but the species composition was quite different in comparison with old growth forest sites, suggesting that enrichment planting will be necessary to restore the original composition. Exotic species were some of the most abundant species in the secondary forest, but their long-term impact depended on life history characteristics of each species. These data demonstrate that one restoration strategy for tropical forest in abandoned pastures is simply to protect the areas from fire, and allow natural regeneration to produce secondary forest. This strategy will be most effective if remnant forest (i.e., seed sources) still exist in the landscape and soils have not been highly degraded. Patterns of forest recovery also suggest strategies for accelerating natural recovery by planting a suite of generalist species that are common in recently abandoned pastures in Puerto Rico and throughout much of the neotropics.

Key words: Caribbean, exotics, secondary succession, tropics.

Introduction

High diversity tropical forests are often deforested for conversion to agriculture. Large areas of tropical dry forests in Central America have been converted to cotton plantations, montane forests have been converted to coffee plantations, lowlands have been converted to banana and sugar cane plantations, and mangroves have been converted to ponds for aquaculture. However, conversion to pastures for cattle grazing is by far the most important land use that has affected tropical forests (Anderson 1990; Hecht 1993). Large areas extending from lowland to montane forest and from dry to wet forest have been used for cattle ranching. Contrary to previous ideas that low nutrient levels of tropical soils would restrict these activities on a site to only a few years (Richards 1964), some agricultural practices have continued for years or even decades on the same site (Uhl et al. 1988; Reiners et al 1994; Aide et al. 1996; Cavelier et al. 1998). Even though sites may be used for many years, some are eventually abandoned because of reduced productivity, economic changes, or socio-political changes (Thomlinson et al. 1996).

Once abandoned, what is the fate of these pastures? Will secondary forests recover to a state similar to the original forests, or will these areas develop into distinct habitats? Previous research has demonstrated that many factors influence the recovery of forest structure and species composition following abandonment of agriculture. An extreme case is slash-and-burn agriculture, which affects only a small area (1–2 ha) for a short period (<2 yr) and occurs in a forest dominated landscape resulting in rapid forest recovery (Uhl 1987). At the other extreme are sites that have been used for many

[1]Department of Biology, University of Puerto Rico, P.O. Box 23360, San Juan, Puerto Rico 00931–3360, U.S.A.
[2]Institute for Tropical Ecosystem Studies, University of Puerto Rico, San Juan, Puerto Rico 00936, U.S.A.
[3]Department of Biology, Valdosta State University, Valdosta, GA 31698, U.S.A.
[4]Department of Biological Science, University of Puerto Rico, P.O. Box 23323, San Juan, Puerto Rico 00931–3323, U.S.A.

years, have suffered extreme soil degradation, experienced frequent fires, and occur in a highly fragmented landscape. Once abandoned, these conditions inhibit the recovery of the original forest and can result in a distinct ecosystem (Aide & Cavelier 1994; Cavelier et al. 1998). Most land use practices and the initial conditions at the time of abandonment of many tropical sites fall between these extremes. In these cases, are tropical forests resilient (Holling 1973; Brown & Lugo 1990, 1994) or are they fragile ecosystems that are unable to recover following human disturbances (Richards 1964; Gómez-Pompa et al. 1972)?

Ecological restoration of tropical forest is a challenging task, but given the high biodiversity of these forests and their influence on global water and carbon cycles (Brown 1993; Phillips et al. 1998), it is critical that we understand how to manage and restore them. Information from many different sources including experience of tropical foresters (Wadsworth 1997) and studies of forest recovery after natural disturbances (Denslow 1987; Walker et al. 1991, 1996) will help us design successful restoration strategies for tropical forests.

In this paper, we describe the pattern of natural forest regeneration in abandoned pastures in Puerto Rico that vary from 5 to 75 years since abandonment. If secondary forest can recover structure and composition within a reasonable time, this low cost strategy could allow us to restore areas that are large enough to have an impact on regional biodiversity and water and carbon budgets (Fig. 1). We assess this approach by addressing the following questions: 1) What is the rate of natural regeneration? 2) How can we accelerate forest recovery? 3) What set of forest species are absent from old pasture sites? and 4) How do exotic species affect the patterns of forest recovery? These questions are addressed by analyzing data from studies of forest regeneration of abandoned agricultural lands in four regions of Puerto Rico (Table 1; Fig. 2).

The Caribbean island of Puerto Rico presents an excellent opportunity to study long-term (50–80 years) tropical secondary forest regeneration. At the beginning of the twentieth century, greater than 90% of Puerto Rico was in some form of agriculture, and remnant forests were limited to small patches. Since the 1940s most of these agricultural areas have been abandoned as the island's economy shifted from agriculture to small industry (Dietz 1986; Birdsey & Weaver 1987) and today, much of the island is covered in secondary forest. This change in land use has produced a chronosequence of secondary forests derived from pasture on soils and lifezones typical of the highly deforested areas in other areas of the Caribbean and neotropics.

Study Regions

Secondary forest derived from abandoned pastures and old forest sites was sampled in four regions (Carite,

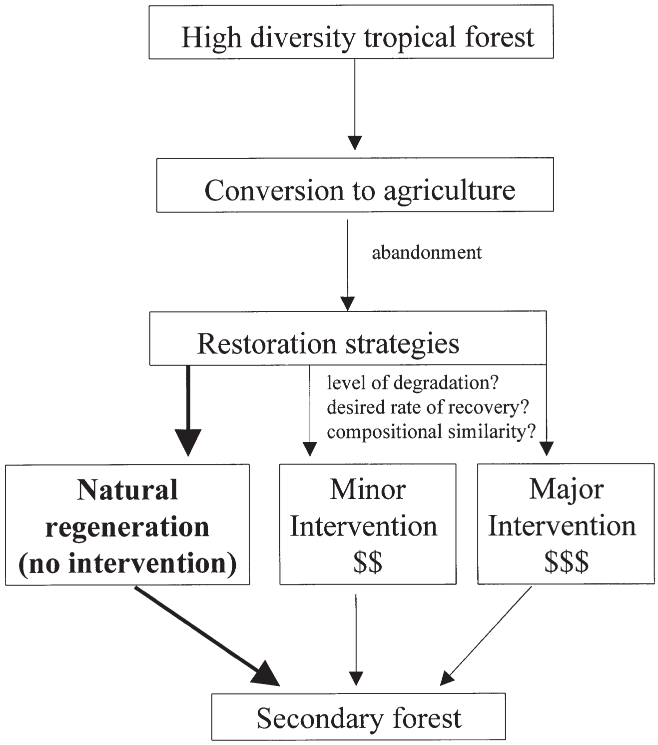


Figure 1. Management strategies for restoration of tropical forest following the abandonment of agricultural lands. Bold arrows represent the strategy that is evaluated in the present study.

Ciales, Luquillo, Utuado) of Puerto Rico (Table 1; Fig. 2). Sixty-four abandoned pasture sites that ranged in age from 5–75 years were sampled, but sites older than 40 years were located only in Luquillo and Carite. Seven old forest sites (>80 years) were sampled in Luquillo and Carite.

During the first half of the twentieth century, the major agricultural activities in the Luquillo region were sugar cane and pastures in the coastal plains (Thomlinson et al. 1996), and pastures and coffee plantations in the mountains (Wadsworth 1950; Garcìa-Montiel & Scatena 1994; Zimmerman et al. 1995). In Luquillo, all cane and coffee plantations have been abandoned, but active pastures still exist in the region. In the Carite region, the major agricultural activities were sugar cane, coffee plantation, and pastures, but presently pastures are the only common agricultural land use (Pascarella et al. 2000). The Utuado study sites occur in one of the most important coffee growing regions of Puerto Rico. Although coffee production has decreased dramatically since the 1920s, this area continues to be one of the most important coffee growing regions (H. Marcano-Vega, unpublished data). Presently, the region is dominated by secondary forests, coffee plantations, pastures, and urban areas (H. Marcano-Vega, unpublished data). The soils

Table 1. Description of the study regions.

Study Region	Geology	Life Zone[a]	Precipitation (mm)	Elevation (masl)	Age of Abandoned Pastures and Forest Sites (yr) <20	20-40	40-60	60-80	>80	Total
Luquillo	Tuffs	Subtropical moist and wet	1500–3500	10–600	9	5	1	6	3	24
Carite	Tuffs/plutonic	Subtropical moist and wet	1520–2540	300–710	8	8	4	4	4	28
Utuado	Tuffs/plutonic	Subtropical wet	2000–4000	160–340	1	7	0	0	0	8
Ciales	Limestone	Subtropical moist	2074	90–300	6	5	0	0	0	11
Total					24	25	5	10	7	71

[a] Lifezone classification is from Ewel and Whitmore (1973).

and topography of the limestone karst region of Ciales are very different in comparison with the other study regions (Table 1; Fig. 2). The karst region is characterized by sink-holes, caves, cliffs, alluvial terraces (long narrow valleys), and mogotes (limestone hills). Although agricultural activities were limited to the valleys where soil has accumulated, forests on the steep slopes and tops of mogotes were also cut for charcoal production (Murphy 1916).

Methods

Aerial photographs from 1936, 1951, 1964, 1977, 1983, 1988, and 1995 were used to select and date individual sites in each of the regions. Site age was determined by taking the mid-point between the last photograph with pasture and the first photograph with shrubs or small trees. Old forest sites were areas with forest cover in the 1936 aerial photographs. It is possible that these areas were used in the past, but given that they had a closed canopy in 1936, they were at least 20 years old and, thus, we have aged these sites as older than 80 years.

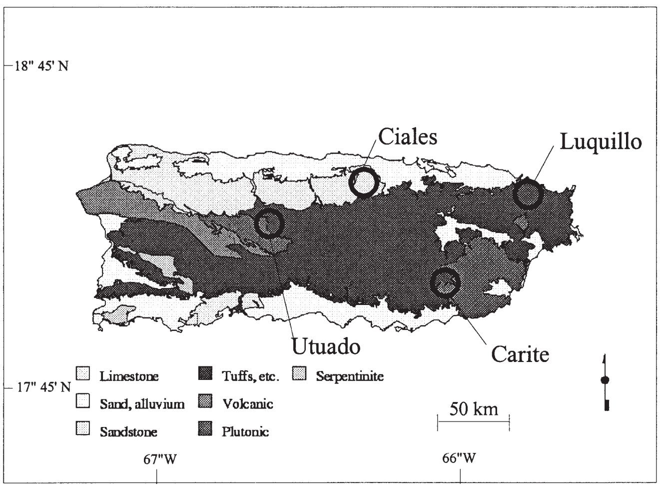


Figure 2. The geology of Puerto Rico and the location of the four study regions.

In Luquillo, Carite, and Utuado, two sampling schemes were used to describe the woody vegetation (Aide et al. 1996; Pascarella et al. 2000; H. Marcano-Vega, unpublished data). Vegetation between 1–10 cm dbh was sampled in four parallel 1 × 50 m transects. Vegetation greater than 10 cm dbh was sampled in two 10 × 50 m transects between the four parallel transects. In the karst valleys of Ciales, woody vegetation greater than 1 cm dbh was sampled in two to five 2 × 50 m transects. The number of transects depended on the width of each valley (Rivera & Aide 1998). Woody vines were not sampled in any of the four regions. Nomenclature follows Liogier (1985, 1988, 1994, 1995, 1997).

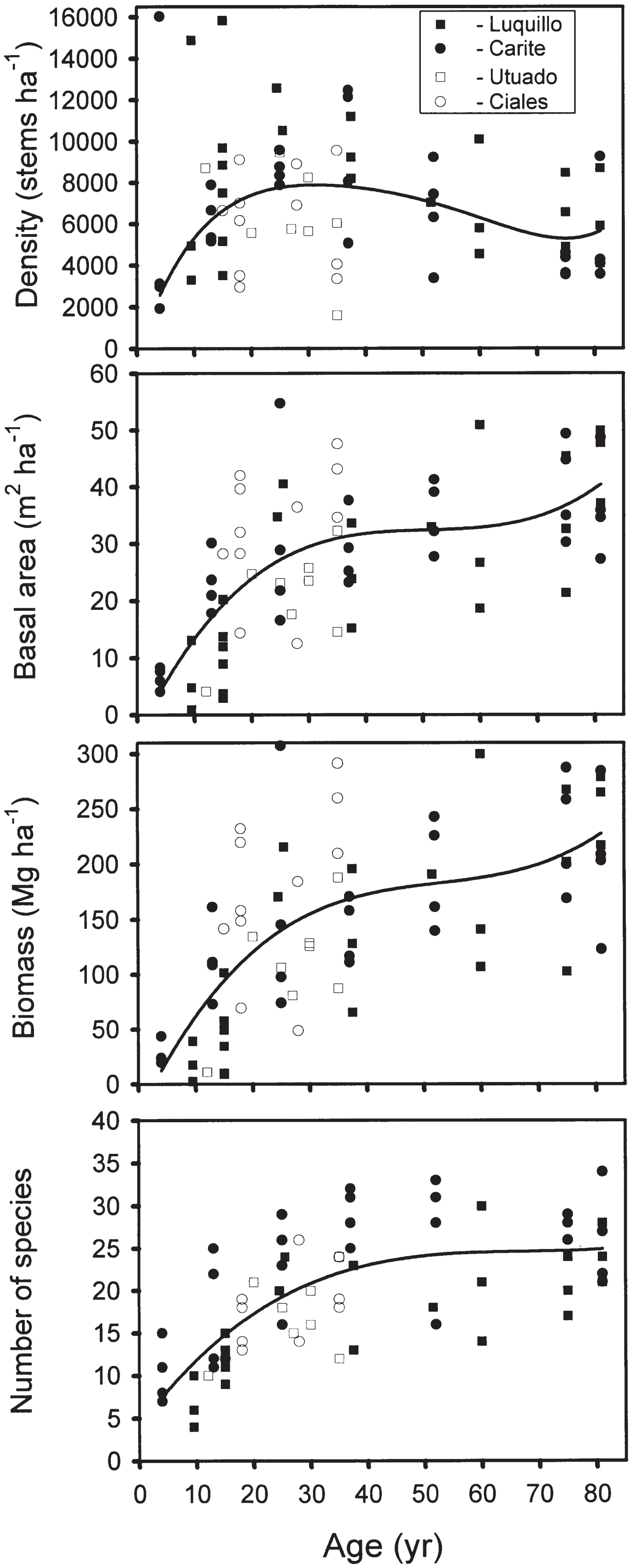
To determine if forest structure, density, basal area, biomass, and number of species had recovered to levels similar to older sites, values were compared between intermediate (35–40 yr) and old (>70 yr) sites using a Student's *t*-test. Biomass was calculated using tree diameters and equations from Weaver and Gillespie (1992).

The recovery of species composition was analyzed using non-metric multidimensional scaling (NMDS) (McCune & Medford 1997). In this analysis, we compared species densities for individuals less than 10 cm dbh and species densities for individuals greater than 10 cm dbh among twelve sites (four 52 yr, four 77 yr, and four >80 yr) from the Carite region. All sites occurred at similar elevations (625–710 masl).

Results and Discussion

Natural Regeneration Without Intervention

We combined data from four regions of Puerto Rico to examine the recovery of forest structure following pasture abandonment (Fig. 3). All regions had sites less than 40 years old, but the oldest sites were found only in Luquillo and Carite (Table 1). Structural characteristics of abandoned pastures were within the range of values of old growth forest after approximately 40 years of regeneration (Fig. 3). Density in the abandoned pastures increased rapidly during the first 25 years, reaching a peak (8,000–10,000 stems/ha) between 25–35 years after



abandonment. The high densities (>14,000 stems/ha) in three sites was mainly due to coppicing of *Miconia prasina*, suggesting that the understory was cut after the site was abandoned. Although there was a trend for density to decrease as forests aged there was no significant difference between the densities of sites 35–40 years and sites older than 70 years ($t = 1.82$, $p = 0.08$).

Basal area also increased rapidly during the first 25 years (Fig. 3). The average basal area in 35–40 yr sites (30 m^2/ha) was significantly lower than the basal area in the sites older than 70 years (39 m^2/ha; $t = 2.31$, $p = 0.03$), but many sites had recovered basal area equal to or greater than the older sites. The aboveground biomass of these sites increased at a rate of 4.9 mg ha^{-1} yr^{-1} during the first 40 years. The average aboveground biomass in the 35–40 yr sites and older than 70 yr sites were 165 mg/ha and 220 mg/ha, respectively.

Species richness in the abandoned pastures increased to an average of 22.6 species per site after 35–40 years (Fig. 3). The species richness in these plots was not significantly different from that of sites greater than 80 yr old (25 spp.; $t = 1.06$, $p = 0.3$).

After approximately 40 years of natural regeneration, the structural characteristics of the secondary forest are similar to the oldest sites in Luquillo and Carite, suggesting that natural regeneration can be an effective strategy for tropical forest restoration. Other studies in Puerto Rico (Zimmerman et al. 1995) and Central America (Finegan 1992, 1996; Guariguata et al. 1997) have described similar results of rapid recovery of forest structure. The recovery of forest structure has important implications for ecosystem functions, such as biomass accumulation and nutrient cycling (Lugo 1992). Few data exist on below-ground changes in carbon pools in abandoned pastures, but our results demonstrate that, with no intervention, abandoned pastures can rapidly become carbon sinks, sequestering approximately 2.5 mg C ha^{-1} yr^{-1}. Natural regeneration will be most successful as a restoration strategy if soils have not been highly degraded and if fires can be controlled, particularly in dry forest, where a single fire can eliminate years of forest regeneration (Janzen 1988). This low cost strategy makes it particularly attractive for large-scale projects with little financial support. A limitation to this approach is that, although woody plant diversity in 35–50 yr old sites was similar to the older sites, it may take hundreds of years for the species composition to recover (Zimmerman et al. 1995).

Figure 3. Relationship between time since abandonment and forest characteristics (density, basal area, biomass and species richness) in 71 abandoned pastures and old forest (>80 yr) sites in Puerto Rico. The three sites with densities greater than 14,000 stems/ha were excluded from the regression.

Table 2. The most common species in 24 abandoned pastures less than 20 years.

				<10 cm dbh		>10 cm dbh		
Species	*Family*	*Growth Form*	*Dispersal*	*Density[a] (ind./ha)*	*Frequency[b]*	*Density (ind./ha)*	*Frequency*	*Elevation Range (masl)*
Miconia prasina	Melastomataceae	Shrub	bird	2913	0.58	10	0.08	20–620
Tabebuia heterophylla	Bignoneaceae	Tree	wind	1065	0.42	126	0.33	30–620
Spathodea campanulata	Bignoneaceae	Tree	wind	1051	0.63	321	0.54	20–550
Psidium guajava	Myrtaceae	Shrub	bird	823	0.38	17	0.08	10–620
Casearia sylvestris	Flacourtiaceae	Small tree	bird	752	0.71	11	0.13	10–550
Casearia guianensis	Flacourtiaceae	Small tree	bird	637	0.63	10	0.04	10–550
Guarea guidonia	Meliaceae	Tree	bird	514	0.46	80	0.21	20–325
Andira inermis	Leguminosae	Tree	bat	274	0.75	57	0.58	30–550

[a] Densities are the mean densities of the sites where the species occurs.
[b] Frequency is the proportion of the sites where the species occurs.

Dominant Species of Recently Abandoned Pastures

Although natural regeneration can produce a secondary forest similar in structure to old forest in approximately 40 years, in certain situations it may be desirable to accelerate recovery to control erosion, increase biodiversity, or promote other ecological interactions. In many tropical sites, poor seed dispersal (Aide & Cavelier 1994; Wunderle 1997; Holl 1998), competition with herbaceous vegetation (Aide et al. 1995), soil compaction and low soil nutrients (Reiners et al. 1994), or photoinhibition (Montaña-Ruiz 1998) can inhibit the initial establishment of woody species. In this section, we determine which shrubs and trees are the most successful colonizing species of recently abandoned pastures. If we can accelerate the establishment of these species, which are capable of growing in recently abandoned pastures, they will shade out herbaceous vegetation and open up the understory for the colonization of woody species that disperse into the site.

Of the more than 200 shrub and tree species identified in the abandoned pastures, only a small subset was common in the recently abandoned pastures (<20 yr) (Table 2). With the exception of *Tabebuia heterophylla*, which is native to Puerto Rico and the Lesser Antilles, all other dominant colonizing species occur throughout the Caribbean and most of the neotropics. In addition, all species except *Guarea guidonia* occur over a broad elevation gradient (near sea level to over 500 masl). The most common species was the shrub *Miconia prasina*, which was found at high densities (approximately 3,000 stems/ha) and in the majority of young sites. This species has rapid growth in abandoned pastures, spreads vegetatively, and produces abundant fruit crops resulting in millions of seeds (J. Pascarella, unpublished data). The second and third most common species, *Tabebuia heterophylla* and *Spathodea campanulata*, produce large numbers of seeds that are wind-dispersed. Larger individuals (>10 cm dbh) of these two species were also found in the recently abandoned pastures, demonstrating a potential for rapid growth. The next three most common species, *Psidium guajava*, *Casearia sylvestris*, and *C. guianensis*, are all bird dispersed and have the capacity to resprout after being cut. The large seeds of *Guarea guidonia* and *Andira inermis* are dispersed by birds

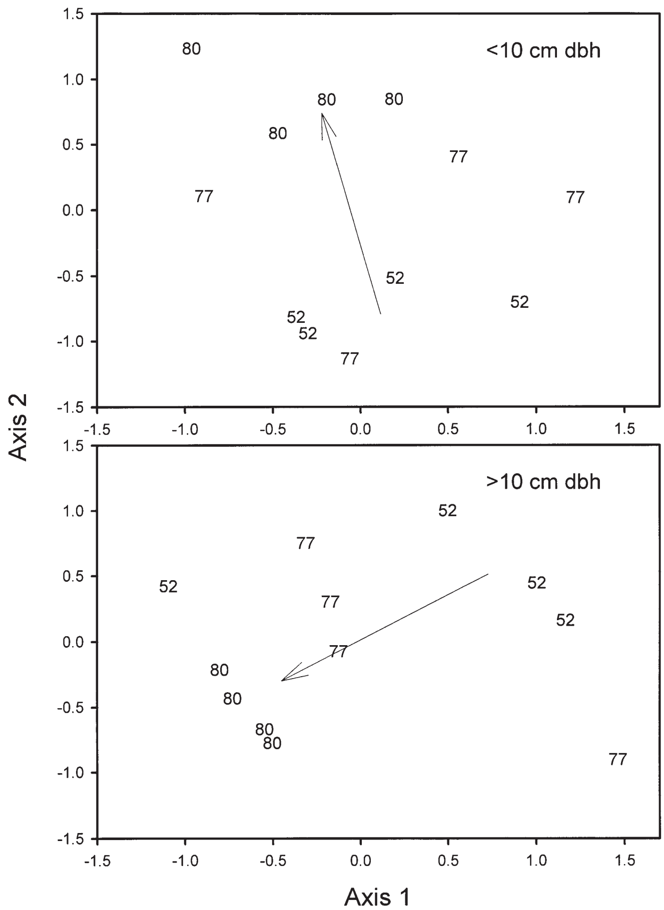


Figure 4. Nonmetric multidimensional scaling of species composition for 12 sites (four 52 yr abandoned pastures, four 77 yr abandoned pastures, and four forest sites >80 yr) from the Carite region.

Table 3. The number of sites where each species is present in four 52-year-old and four 77-year-old abandoned pastures and four old growth forest sites (>80 yr) in Carite.*

		< 10 cm dbh			>10 cm dbh		
Species	*Family*	*52 yr*	*77 yr*	*>80yr*	*52 yr*	*77 yr*	*>80 yr*
Ocotea leucoxylon	Lauraceae	4	4	4			
Cordia borinquensis	Boraginaceae	4	3	4			
Myrcia deflexa	Myrtaceae	3	4	3			
Syzygium jambos	Myrtaceae	0	3	3			
Guarea glabra	Meliaceae	0	2	3			
Dacryodes excelsa	Burseraceae	1	0	4	1	0	4
Miconia tetandra	Melastomataceae	1	0	4	0	0	4
Drypetes glabra	Euphorbiaceae	0	1	4	0	0	4
Micropholis guyanensis	Sapotaceae	0	1	3	0	1	4
Sloanea berteriana	Eleocarpaceae	0	1	3	0	1	4
Prestoea montana	Arecaceae				4	4	4
Alchornea latifolia	Euphorbiaceae				4	3	2
Schefflera morototoni	Araliaceae				3	3	4
Casearia arborea	Flacourtiaceae				3	3	4
Homalium racemosum	Flacourtiaceae				0	2	4
	# of species in at least 50% of the sites	3	5	10	4	5	10

*The species selected had the highest 10 densities in the <10 cm dbh or >10 cm dbh size classes.

and bats, respectively, and produce large seedlings that have high survivorship in the pastures (Zimmerman et al. 2000). These two species are of additional interest, given that they are potential timber species. Two of the most common species, *Spathodea campanulata* and *Psidium guajava*, were exotics and are discussed in more detail in the following section.

The extensive geographical and elevational distribution of these species suggests that they should be excellent candidates for restoration projects throughout much of the neotropics. Although a few other species disperse into abandoned pastures (Zimmerman et al. 2000), there appear to be other barriers that inhibit their colonization. The successful colonization by this subset of species appears to be due to different combinations of characteristics (e.g., large seeds, wind-dispersed seeds, vegetative growth, ability to resprout). If these colonizing species can be established early by seeding, planting seedlings, or releasing existing individuals, they may be able to accelerate forest regeneration by providing habitat and food for dispersers of other forest species and a microhabitat appropriate for their establishment.

Comparison of Species Composition Between Old Abandoned Pastures and Old Forest Sites

The goal of restoration projects should be not only to recover forest structure but also native species composition. Unfortunately, most of the native vegetation in the lowlands of Puerto Rico was eliminated before detailed botanical studies had been conducted (Cook & Gleason 1928; Wadsworth 1950). Thus, to achieve this goal in lowlands of Puerto Rico, one would have to make some assumptions regarding the composition of mature forest. Even with these limitations, an analysis of species composition can help to identify important forest species that are not colonizing secondary forest.

To better understand the recovery of species composition, we compared species abundance of four 52 yr old and four 77 yr old abandoned pastures with four old forest sites, all from similar elevations in the Carite region. The results show that species composition of old secondary forest (52–77 yr) derived from abandoned pastures was very different in comparison with old growth sites (>80 yr) (Fig. 4). This is true for the larger individuals (>10 cm dbh), as well as the smaller individuals (<10 cm dbh). Of the 10 most common species in the juvenile size class (<10 cm dbh) in the old forest sites, only three species, *Ocotea leucoxylon*, *Cordia borinquensis*, and *Myrcia deflexa*, occurred in at least 50% of the secondary forest sites derived from 52 yr abandoned pastures (Table 3). After an additional 25 years of regeneration, only 5 of the 10 most common species occurred in at least 50% of the 77 yr sites. A similar pattern was observed for the 10 most common species in the adult size class (>10 cm dbh) (Table 3). Only four and five of the most common species occurred in at least 50% of the 52 yr and 77 yr sites, respectively. These data suggest that it will take many years for the species composition to converge with that of the old forest.

With the exception of Ciales, all study sites occurred in subtropical moist or wet lifezones (Ewel & Whitmore 1973) on volcanic-derived substrates, where three of the most important species of old forest are *Dacryodes excelsa*

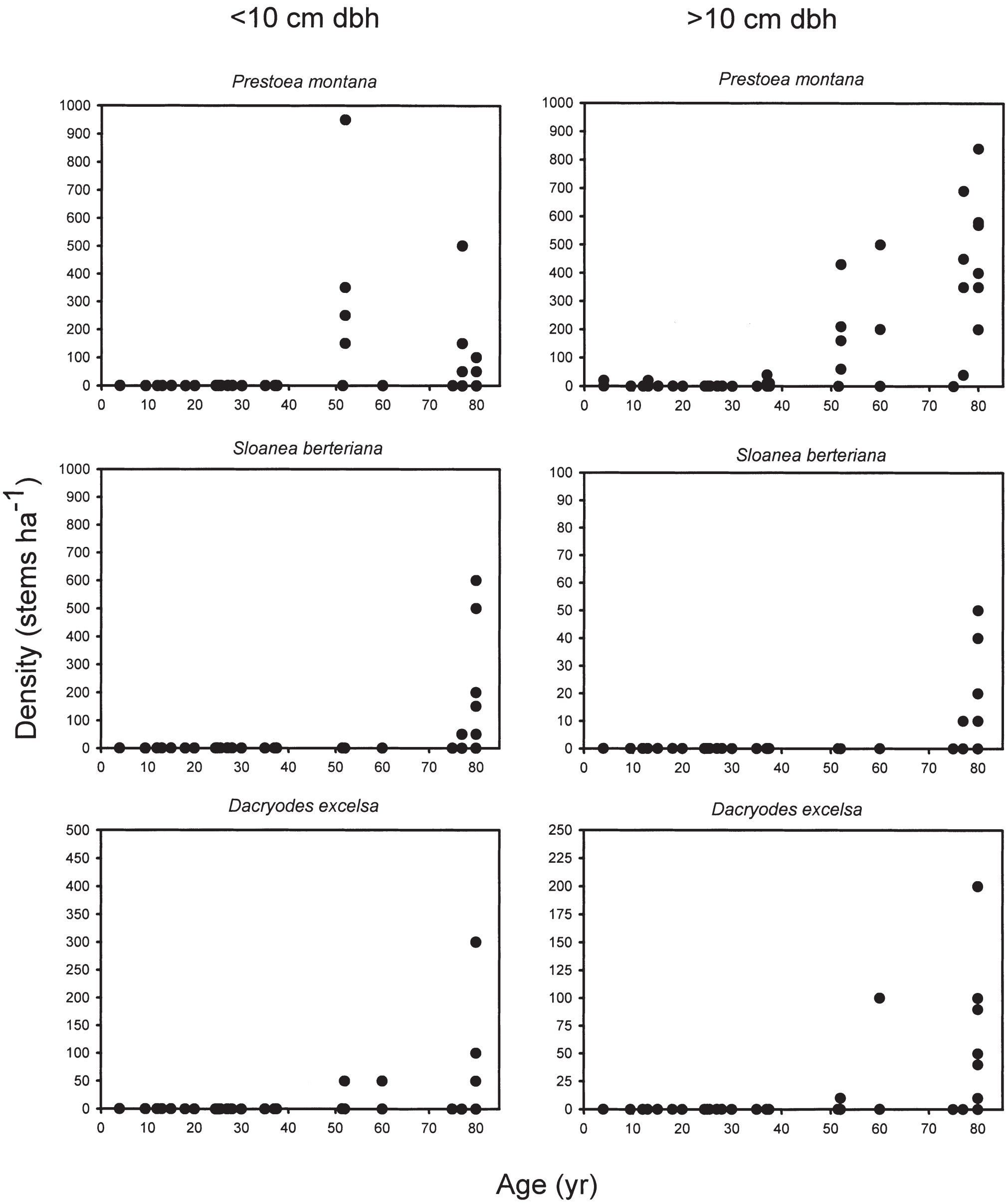


Figure 5. Densities of juveniles (<10 cm dbh) and adults (>10 cm dbh) of *Prestoea montana*, *Sloanea berteriana*, and *Dacryodes excelsa*, three important tree species of old growth forest, in 71 abandoned pastures and old forest (80 yr) sites. Note that the scale of the y-axis varies among panels.

(tabonuco), *Prestoea montana* (sierra palm), and *Sloanea berteriana* (Cacaìllo) (Wadsworth 1950; Little & Wadsworth 1964; Odum & Pigeon 1970). Of these three species, the palm, *P. montana*, had the highest densities in the secondary forests but, as with the other two species, it was virtually absent from secondary forest (<40 yr) (Fig. 5). In general, individuals of *D. excelsa* and *S. berteriana* were isolated in the oldest forest on the island and dispersal into neighboring secondary forest has been very limited (Fig. 5). These species often occur in forest stands within 100–200 m of secondary forest, but their absence in secondary forest (>50 yr old) strongly suggests that dispersal is a major factor limiting colonization. Poor dispersal could be due to the extinction of important seed dispersers/predators (e.g., Puerto Rican crow, jutia-large rodent) or to population reduction of important seed dispersers/predators (e.g., Puerto Rican parrot). Other factors that could limit the species' ability to establish in these secondary forests are low seed production due to small population size (inbreeding) or loss of pollinators.

These results demonstrate that, if the goal of a restoration project is to restore the species composition similar to that of the oldest sites, it will be necessary to do enrichment planting. However, if interactions such as pollination, dispersal, and predation have been lost, then planting may not be sufficient to insure the long-term ecological functioning of these forests.

Effect of Exotic Species on Forest Recovery

Invasions by exotic plant species can alter forest structure, composition, and dynamics (Vitousek et al. 1997;

Horvitz et al. 1998), and island habitats have been particularly vulnerable to exotic plant species (Smith 1984). For example, in Tahiti, *Miconia calvescens* has invaded the few remaining stands of natural forest (Meyer & Florence 1996). In an effort to reforest large areas of Puerto Rico, between 1936–1949 the U.S. Forest Service introduced approximately 10 million seedlings of 17 exotic species (Marrero 1950). How has the introduction of these exotic species affected forest recovery?

Only three exotic species, *Spathodea campanulata*, *Psidium guajava*, and *Syzygium jambos* occurred in more than 10% of the sites (Table 4) and none of these species was planted by the U.S. Forest Service (Marrero 1950). *S. campanulata* is a large tree that has wind-dispersed seeds. Smaller individuals (<10 cm dbh) occurred in 44% of the sites and larger individuals (>10 cm dbh) occurred in 38% of the sites. *S. campanulata* occurred over a large elevational gradient and was mainly restricted to forest stands less than 35 years old. This species was introduced as a shade tree and ornamental (Little & Wadsworth 1964). *Psidium guajava* is a shrub or small tree that has an edible fruit that is often dispersed by cattle and, thus, can be an important colonizer of pastures. Smaller individuals occurred in 19% of the sites and larger individuals occurred in only 3% of the sites. Like *S. campanulata*, *P. guajava* occurred across a large elevational gradient and was found only in young secondary forest (<35 yr). *Syzygium jambos* was another important exotic species in the secondary forest, but this species was not restricted to the youngest forest. In fact, in a number of cases, it has invaded old forest sites.

S. campanulata and *S. jambos* both occurred in many sites and at high densities. Given that both species are trees, their impact on the secondary forest could be substantial. Although *S. campanulata* is the species with the highest basal area in Puerto Rico (Franco et al. 1997), it was not an important component of secondary forest (>40 yr) (Fig. 6). This species is an excellent colonizer of abandoned pastures (Rivera & Aide 1998), but given that it is shade intolerant, it does not recruit in the understory. *S. campanulata* appears to live 30–40 yr (Fig. 6) and once it dies out it is replaced almost exclusively by native tree species, suggesting that this species may facilitate the recovery of forest in Puerto Rico. The dynamics of *S. jambos* are very different in comparison with *S. campanulata. S. jambos* occurred in sites of all ages and the highest densities of both small and large individuals were in the oldest sites. The recruitment of smaller individuals in the older sites suggests that this species will remain in these forests for hundreds of years. The large seed of *S. jambos* produces a large seedling that can survive and grow in the shaded understory (Horvitz et al. 1998). In addition, *S. jambos* can reproduce vegetatively, a characteristic that has allowed this species to colonize the riparian zone throughout Puerto Rico (Little & Wadsworth 1964). Once adults of *S. jambos* have established, the dense canopy produces low light levels in the understory that restricts the colonization of more light-demanding species (Little & Wadsworth 1964; Horvitz et al. 1998). In summary, large shade-tolerant seedlings, vegetative reproduction, and dense canopy appear not only to allow *S. jambos* to survive in older sites but to invade forest and inhibit the colonization of native species.

The impact of these species on forest recovery has much more to do with life history characteristics than the geographical origin of a species. Native species that were planted or established in high densities can also inhibit the establishment of native forest (*Alnus acuminata*; Cavelier 1995; Murcia 1997). In the case of Puerto Rico, the dominance of *S. campanulata* in the second forest may be seen as a major problem, but our data suggest that as these forests age, *S. campanulata* will become less important and will be replaced by native species. Without any intervention, the wind-dispersed seeds of *S. campanulata* have colonized many abandoned pastures, shading out the grasses and herbaceous vegetation, and providing a habitat appropriate for the colonization of many native tree species. Although *T. heterophylla*, a wind-dispersed native species with a higher quality timber (Little & Wadsworth 1964) could fill this role, it is not clear if the cost to increase the presence of this

Table 4. Common exotic species in 71 abandoned pasture and forest sites.

				<10 cm dbh		>10 cm dbh			
Species	*Family*	*Growth Form*	*Dispersal*	*Density*[a] *(ind./ha)*	*Freq.*[b]	*Density (ind./ha)*	*Freq.*	*Age of Forest Stands*	*Elevation Range (masl)*
Spathodea campanulata	Bignoniaceae	tree	wind	863	0.44	276	0.38	<35 yr	20–670
Psidium guajava	Myrtaceae	shrub	animal	527	0.19	17	0.03	<35 yr	10–620
Syzygium jambos	Myrtaceae	tree	animal	464	0.38	88	0.22	yg-old	30–710
Coffea arabica	Rubiaceae	shrub	animal	128	0.08	0	0.00	yg-old	90–700
Tectona grandis	Verbenaceae	tree	wind	137	0.06	13	0.04	<35 yr	160–210
Spondias mombin	Anacardiaceae	tree	animal	30	0.04	30	0.06	yg-old	50–350

[a]Densities are the mean densities of the sites where the species occurs.
[b]Frequency is the proportion of the sites where the species occurs.

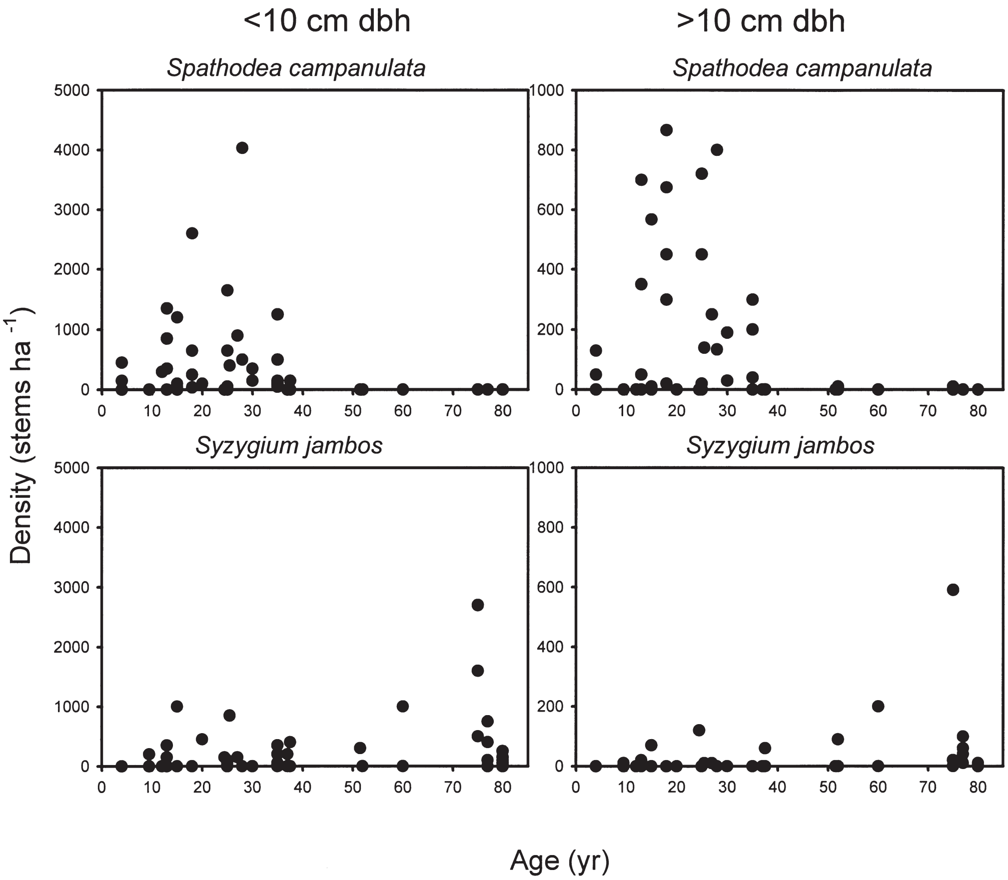


Figure 6. Densities of juveniles (<10 cm dbh) and adults (>10 cm dbh) of the two most common exotic tree species, *Spathodea campanulata* and *Syzygium jambos*, in 71 abandoned pastures and old forest sites (>80 yr). Note that the scale of the y-axis is different for <10 cm dbh and >10 cm dbh panels.

species over that of *S. campanulata* would be worth the additional effort. The impact of *S. jambos* has been quite different. It has invaded riparian areas and old growth forest stands and appears to inhibit the regeneration of native forest species. To recover native forest in areas that are dominated by *S. jambos*, it will be necessary to reduce the abundance of this species.

Synthesis and Conclusions

The restoration of high diversity tropical forest following the abandonment of agricultural lands provides a challenge for restoration ecologists. The appropriate restoration strategy depends on the level of degradation, the desired rate of recovery and the desired similarity to species composition of native forest (Fig. 1). The results from our research demonstrate that natural regeneration can be an effective strategy for restoration of tropical secondary forest. Recovery of forest structure, including woody tree species diversity, occurred in approximately 40 years. This restoration strategy will be most effective if soils have not been severely degraded, if fires can be suppressed, and if remnant forests (i.e., seed sources) are in the landscape. The low cost of managing natural regeneration makes this strategy a potential option, particularly for restoration of large areas.

If the goal of a project is not only to recover forest structure but also species composition similar to the original forest, additional intervention will be necessary (Fig. 1). Many old forest species exist in the landscape but are not colonizing the secondary forest derived from abandoned pastures. These species are often shade tolerant and, thus, enrichment plantings of seedlings may be sufficient for establishment. This additional effort will increase the costs of a project, but it appears to be necessary given the poor colonization of these species after more than 60 years of natural regeneration.

It is important to note that, in our study, the size of the pastures and distance to seed sources were small and soil degradation was not severe. Furthermore, tree biodiversity is much lower in Caribbean forest compared with the mainland. These conditions have facilitated forest recovery. In many other areas of the neotropics, pastures are much larger (100–1000 ha) and dispersal limitation will be greater. In these areas, a greater effort will be needed to establish trees and shrubs after abandonment, and enrichment planting will be essential to establish forest tree species.

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