Available online at www.sciencedirect.com

SCIENCE DIRECT®

Forest Ecology and Management 188 (2004) 1–15

Forest Ecology and Management

www.elsevier.com/locate/foreco

The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica

Daniela Cusack, Florencia Montagnini*

School of Forestry and Environmental Studies, Yale University, 370 Prospect St., New Haven, CT 06511, USA

Received 16 February 2003; received in revised form 28 March 2003; accepted 15 June 2003

Abstract

Tropical timber plantations provide a variety of environmental services, including recovery of biodiversity on degraded lands. For example, plantations can speed forest successional processes by improving microsite conditions and attracting seed dispersers, thus promoting woody regeneration. Timber species have been hypothesized to differ in understory recruitment success. In the present research, understory regeneration of woody plants was compared for six native timber species on tropical plantations in the Atlantic humid lowlands of Costa Rica. Timber species compared were: *Calophyllum brasiliense* Cambess, *Hieronyma alchorneoides* Allemao, *Terminalia amazonia* (J.F. Gmel.) Exell, *Virola koschnyi* Warb., *Vochysia ferruginea* Mart., and *Vochysia guatemalensis* Sprague. The six species were present at each of the three sites: one experimental plantation and two small-scale plantations belonging to farmers of the region. All plantations were 9–10 years. The experimental plantation was 100 m from continuous forest (i.e., seed source), and the farmers' plantations were 1.3 and 2.5 km from continuous forest. Four plots were sampled for each timber species at each site using a randomized block design. All understory woody species were counted, identified, and separated by height class. Canopy openness and leaf litter biomass on the plantation floor were also evaluated.

All of the plantations studied showed significantly higher levels of understory regeneration than control plots on abandoned pastures ($P < 0.05$). In this study, plantation site was the most significant factor affecting understory woody species diversity ($P < 0.0001$). Different timber species were most successful at recruiting understory regeneration in each of the three sites. On the experimental plantations at site 1, *V. guatemalensis* and *C. brasiliense* had the greatest recruitment success, with 75,581 and 69,219 regenerating individuals/ha, respectively. In the commercial plantations, *T. amazonia* (16,250 regenerating individuals/ha) had the greatest recruitment success at site 2, and *V. ferruginea* (29,219 regenerating individuals/ha) had the greatest recruitment success at site 3. Across sites, plots with intermediate canopy openness had greater abundance of understory regeneration than plots with low or high percentages of canopy openness ($P = 0.02$). There was no relationship between understory regeneration and leaf litter biomass. Of the planted species most successful at restoring understory diversity, *V. guatemalensis*, *T. amazonia*, and *V. ferruginea* have demonstrated good form and growth for timber, making them important species for reforestation in the region.

Keywords: Biodiversity; Costa Rica; Understory regeneration; Native species plantations

1. Introduction

In the early 1990s, the total area of deforested and degraded tropical land worldwide (2 billion ha)

---

* Corresponding author. Tel.: +1-203-436-4221;
fax: +1-203-432-3929.
E-mail address: florencia.montagnini@yale.edu (F. Montagnini).

0378-1127/$ – see front matter © 2003 Published by Elsevier B.V.
doi:10.1016/S0378-1127(03)00302-5

surpassed the area of mature tropical forests (1.8 billion ha) (Lugo, 1997). In Costa Rica alone, over 50% of the natural forests have been cleared for agriculture and grazing (FAO, 2000), yet the productivity of cleared lands is often short-lived. On pasturelands in advanced stages of degradation, native forest regeneration occurs slowly or not at all (Ashton et al., 2001). Forest successional processes are often hindered, because moderately to severely degraded pasturelands tend to be colonized quickly by invasive grasses and ferns (Kuusipalo et al., 1995). The competitive advantage of grasses, combined with degraded soils and lack of nutrients, often prevents the germination and initiation of tree seedlings (Kuusipalo et al., 1995; Parrotta, 1992).

Various studies have found that plantations of native or exotic timber species can increase biodiversity by promoting woody understory regeneration (Ashton et al., 2001; Carnevale and Montagnini, 2002; Guariguata et al., 1995; Haggar et al., 1997; Keenan et al., 1997, 1999; Kuusipalo et al., 1995; Lugo, 1997; Parrotta et al., 1997; Powers et al., 1997). Plantations promote understory regeneration by shading out grasses, increasing nutrient status of topsoils (through litterfall), and facilitating the influx of site-sensitive tree species (Grubb, 1995). In addition to increasing biodiversity, forest regeneration can restore soil fertility, reduce erosion, reduce fire hazard, and restore biological productivity (Montagnini, 2000; Parrotta, 1992).

Despite the biological success of forest restoration, reforestation projects are often expensive, and therefore unrealistic for wide-scale application in developing countries (Parrotta et al., 1997). In order to make reforestation economically viable, countries like Costa Rica have supported programs that use plantations of fast-growing timber species to ameliorate site conditions and promote natural forest succession. This approach has the advantage that timber species can eventually be harvested, providing an economic incentive for farmers to reforest abandoned pasturelands.

In this study we examined the potential of six native timber species for restoring the diversity of understory woody species in tropical ecosystems. Most previous studies of understory regeneration in Costa Rican plantations have been conducted exclusively in experimental plantations rather than in commercial plantations (Carnevale and Montagnini, 2002; Guariguata et al., 1995; Montagnini, 2000; Powers et al., 1997). We sought to determine whether trends in understory regeneration observed in experimental plantations are similar to trends in commercial plantations of the same timber species.

2. Study site

Three plantation sites were used for this research. All sites were native species plantations established between 1992 and 1993 in the Caribbean lowlands of Costa Rica. The study sites are located at 10°12′–10°47′N latitude and 84°09′–83°45′W longitude. Mean annual temperature is 24 °C. Mean annual precipitation is 3500–4000 mm, and in no month is precipitation less than 50 mm. Elevation is between 30 and 200 m. The overall topography is flat to undulating terrain. In general, soils belong to the Ultisol and Inceptisol orders. There are various limitations of the soil, such as slow or impeded drainage, and very low to medium fertility. These limitations restrict land use in the region to permanent crops and reforestation (Piotto et al., 2003).

The first site used in this study were experimental plantations at La Selva Biological Station. The second and third sites were native species plantations on private farms belonging to Vicente Paniagua and Isidro Quesada. Plantations covered 7.5, 16, and 20 ha, respectively. All sites were bordered by roads; the commercial plantations were bordered by a public highway, while La Selva plantations were bordered by a private, dirt road. Both farmers' plantations were established with technical advising from a local non-governmental organization, FUNDECOR (Foundation for the Development of the Central Mountain Range), as part of a government reforestation initiative.

All plantations were 9–10 years old at the time of this study. All had low-intensity management, with little or no cleaning, clearing or pruning since the third year. Some cleaning did occur on farmers' plantations, but none had occurred for at least 3 years prior to this study. Plantations also had similar thinning regimes, although final spacing varied from 4 m × 4 m to 4 m × 8 m (Table 1). The La Selva plantation was 100 m from continuous forest, the Paniagua plantation was 1.3 km from continuous forest, and the Quesada

Table 1
Plantation information for each of the three study sites

	Basal area (m^2/ha)	Spacing (m × m)	Slope/drainage[a]	Canopy openness (%)
La Selva				
H. alchorneoides	80.6	2 × 4	Flat	12
C. brasiliense	67.5	2 × 4	Flat	16
V. ferruginea	88	4 × 4	Flat/variable drainage	13
V. guatemalensis	142.5	2 × 4	Flat	15
T. amazonia	91.9	2 × 4	Flat	13
V. koschnyi	82.5	2 × 4	Flat	8
Paniagua				
H. alchorneoides	43.1	4 × 8	Flat/poorly drained	8
C. brasiliense	60	2 × 2	5–10% slope	11
V. ferruginea	54.3	4 × 8	Flat	20
V. guatemalensis	46.8	8 × 8	5% slope	10
T. amazonia	43.1	4 × 8	Flat	14
V. koschnyi	41.3	4 × 6	Flat	10
Quesada				
H. alchorneoides	37.5	4 × 4	Flat/poorly drained	13
C. brasiliense	58.1	4 × 4	Flat/variable drainage	11
V. ferruginea	67.5	4 × 6	Flat to 2% slope	15
V. guatemalensis	80.6	6 × 6	Flat	26
T. amazonia	45	4 × 4	Flat	12
V. koschnyi	56.3	4 × 6	Flat to 2% slope/variable drainage	12

[a] If no drainage class noted, assume well drained.

plantation was 2.5 km from continuous forest. None of the sites were connected to each other by continuous forest. Factors which varied between the three sites included: exact distance to continuous forest, final spacing of planted trees, and undulation of terrain (Table 1). The block design of the experiment was expected to account for these major differences between sites. Due to differences in distance to forest, planting design, and management history, however, the sites were not perfect replicates.

Each site had adjacent plantation plots (1–5 ha each) of different timber species. Six species were used in this study, each of which was present at every site. Pure-species plantations of *Calophyllum brasiliense* Cambess, *Hieronyma alchorneoides* Allemao, *Terminalia amazonia* (J.F. Gmel.) Exell, *Virola koschnyi* Warb., *Vochysia ferruginea* Mart., and *Vochysia guatemalensis* Sprague were used as overstory treatments in this study. These species were among the most popular for timber plantations on small- and medium-sized farms in the region (Piotto et al., 2003). Pastures abandoned at the time of planting, and adjacent to each site, were used as controls.

La Selva experimental plantations were arranged in randomized blocks of timber species and natural regeneration plots. On the two farmers' plantations, the six timber species were planted in plots adjacent to each other and adjacent to abandoned pastures. This arrangement created a mosaic of patches which was used in this study as a block design. At each site four subplots of 4 m × 4 m were established for each of the six timber species and the control pastures. In total, 12 subplots were established for each species and the controls, totaling 1344 m^2 surveyed.

3. Methods

3.1. Evaluation of understory woody regeneration

Understory woody regeneration was surveyed in four subplots established for each timber species at each site. Only woody species were recorded. Abundance and species richness in each subplot were recorded using three height classes (Height Class 1: <30 cm; Height Class 2: 30 cm–2 m; Height Class

3: >2 m). Height Class 1 was surveyed in 2 m × 2 m subplots nested within each 4 m × 4 m subplot. Height Classes 2 and 3 were surveyed in the entire 4 m × 4 m subplots.

Regenerating woody individuals were identified to genus or species in the field, and specimens were taken for confirmation of identification at La Selva Biological Station herbarium. Woody species diversity was calculated using the Simpson index and the Shannon–Weiner index for understories of the six timber species. Species composition was also analyzed by assigning seedlings to guilds based on dispersal mechanism. Five dispersal guilds were used: bird, bat, rodent or other mammal, wind, and water or gravity.

3.2. Light availability and plantation floor litter

Understory light availability and leaf litter on the plantation floor were evaluated. Light availability was recorded as a percent of canopy openness, and measured with a handheld spherical densiometer. Readings were taken facing the four directions at the four corners of each subplot. Averages were calculated from the 16 densiometer readings for each subplot. Litter was collected from two 50 cm × 50 cm quadrats in each subplot, oven dried, and weighed.

3.3. Statistical analysis

Because data were count-data of stem occurrence in plots, a Poisson transformation was used to normalize the distribution and means of errors. Abundance data were analyzed using the SAS program General Linear Model. The first model tested for significant differences in understory abundance between control and planted sites. A second model used only data from the six timber treatments, disregarding the control sites, where regeneration was equal to zero. Independent variables used in the final model were timber species, plantation site, canopy openness, leaf litter weight, and all interactions. The dependent variable was number of individuals regenerating. Quadratic and cubic models were used to analyze the relationship between canopy openness and regeneration abundance. Tukey tests were used to compare total regeneration, regeneration by height class, and dispersal mechanism among the six timber species (α for all tests $= 0.05$). Data from all three sites were analyzed both pooled together, and separately by site. SPSS *k*-means clustering was also used to evaluate plot groupings according to dispersal mechanism. The appropriate number of clusters was determined using the Haritgan Rule of Thumb. Membership of individual plots in clusters was examined in relation to site and overstory species.

4. Results

4.1. Total understory abundance

When comparing planted plots to the control plots, all plots with planted species had significantly higher abundance of regenerating individuals than control plots ($P < 0.0001$). Because all control plots had 0 regeneration, these plots were not used for the subsequent analysis.

When data from all three sites were pooled together and analyzed, there was only a significant difference in total abundance of regenerating individuals between the six treatments when the interaction between site and planted species was included in the model. The interaction between site and plantation species was significant ($P < 0.0001$). Once the interaction was accounted for, site had a highly significant association with regeneration ($P < 0.0001$), and planted species had a significant association ($P < 0.02$) with total regeneration.

There was no significant difference between treatments for Height Classes 1 and 2 when all data were pooled together. For Height Class 3, plantations fell into two groupings. *V. guatemalensis*, *T. amazonia* and *V. koschnyi* had significantly more regeneration in Height Class 3 across sites than the other treatments ($\alpha = 0.05$).

4.2. Understory abundance within each site

Fig. 1 shows the total abundance of regenerating individuals in treatments for the three sites. At La Selva experimental plantations, *C. brasiliense* and *V. guatemalensis* had a significantly greater total abundance of regenerating individuals than other species, with 75,581 and 69,219 individuals/ha, respectively. *V. guatemalensis* plantations also had significantly

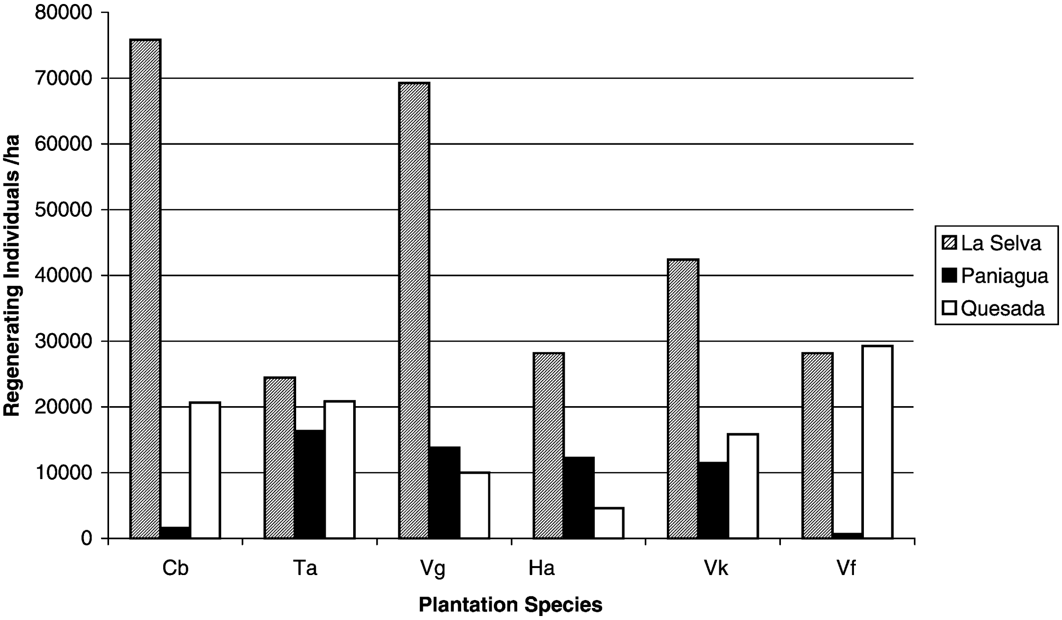

Fig. 1. Total abundance of understory woody regeneration under six timber species at the three study sites. Cb: *Calophyllum brasiliense*, Ta: *Terminalia amazonia*, Vg: *Vochysia guatemalensis*, Ha: *Hieronyma alchorneoides*, Vk: *Virola koschnyi*, Vf: *Vochysia ferruginea*.

higher abundance of Height Class 1 (<30 cm) regeneration. Plots of *C. brasiliense* had significantly higher regeneration of Height Class 2 (30 cm–2 m) than other timber species, and there was no difference among timber species for Height Class 3 (>2 m) (Fig. 2).

At the Paniagua plantation, *T. amazonia* (16,250 individuals/ha), had significantly greater total understory regeneration than other species. *V. guatemalensis* was next with 13,750 individuals/ha. *T. amazonia* had the highest abundance of regeneration for Height

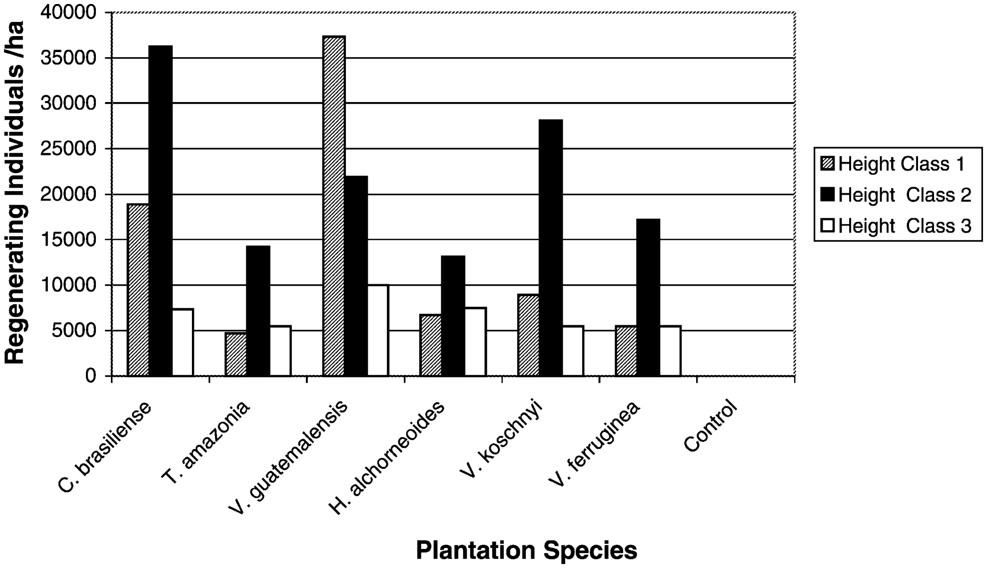

Fig. 2. Understory regeneration in six timber species by height classes at La Selva experimental plantations.

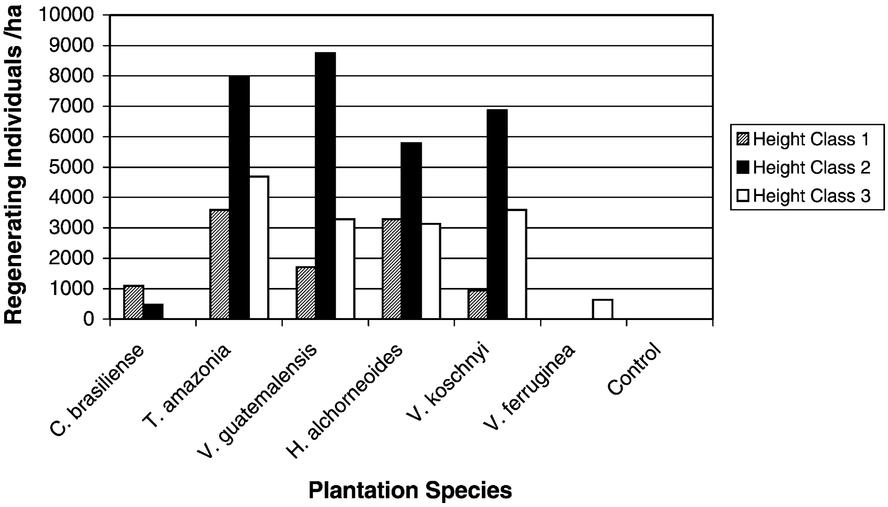

Fig. 3. Understory regeneration in six timber species by height classes at Paniagua plantations.

Class 1. *T. amazonia* and *V. guatemalensis* had significantly more regeneration of woody species in Height Class 2, and *T. amazonia*, *V. guatemalensis* and *H. alchorneoides* had higher abundance of Height Class 3 regeneration than the other three timber species (Fig. 3).

At the Quesada site, *V. ferruginea* (29,219 individuals/ha) had the greatest understory abundance of understory regeneration, followed by *T. amazonia* (20,718 individuals/ha) and *C. brasiliense* (20,625 individuals/ha). *V. ferruginea* had the greatest abundance of understory regeneration for Height Classes 1 and 2. *T. amazonia* and *V. koschnyi* had the most understory regeneration for Height Class 3 (Fig. 4).

4.3. Understory species diversity

Understories were dominated by shrub species of the Melastomataceae (476 individuals total), Piperaceae (360 individuals total), Nyctaginaceae

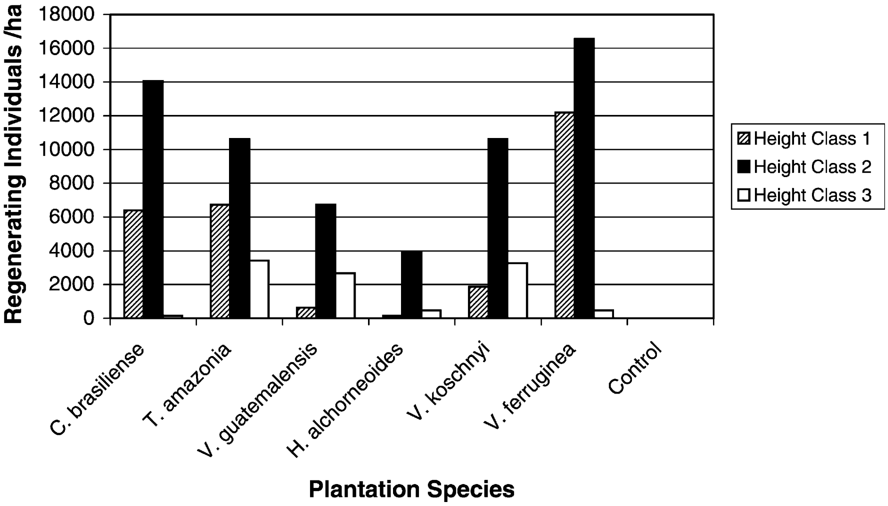

Fig. 4. Understory regeneration in six timber species by height classes at Quesada plantations.

Table 2
Simpson and Shannon–Wiener diversity indices for plantations species (data from the three sites are included)

Treatment	Number of individuals/192 m^2	Number of species/192 m^2	Simpson index	Shannon–Wiener index
C. brasiliense	542	53	0.93	1.36
T. amazonia	393	57	0.93	1.40
V. guatemalensis	603	55	0.88	1.20
H. alchorneoides	288	48	0.92	1.33
V. koschnyi	444	60	0.93	1.39
V. ferruginea	374	49	0.88	1.21
Control	0	0	0	0

(333 individuals total), and/or Rubiaceae (319 individuals total) families (Appendix A). However, 13% of the regeneration across all sites was natural regeneration from seed of a planted timber species. Combined, seedlings of the two Vochysiaceae timber species were the fifth most abundant regeneration in plantation understories (297 individuals total).

Compositions of understories at each site were dominated by a few genera. At each site, five genre or species comprised over 50% of the understory. At La Selva Biological Station, the five most abundant species/genre in the understory were *Neea psychotrioides* Donn. Sm. (18.5%), *Piper* spp. (16.8%), *V. guatemalensis* Sprague (11.2%), *Miconia* spp. (10.6%), and *Psychotria* spp. (8.9%). At the Paniagua plantations, the five most abundant species/genre in the understory were *Clidemia hirta* (L.) D. Don (24.7%), *Rhodostemonodaphne kunthiana* (Nees) Rohwer (16.3%), *Miconia* spp. (9.5%), *N. psychotrioides* Donn. Sm. (7.9%), and *Conostegia subcrustulata* (Beurl.) Triana (7.3%). At the Quesada plantations, the five most abundant species/genre were *V. ferruginea* Mart. (16.3%), *Miconia* spp. (13.6%), *Piper* spp. (10.2%), *Sabicea panamensis* Wernham (6.5%), *C. hirta* (L.) D. Don (5.2%).

Plantations of *V. koschnyi* had the greatest richness of understory species across sites, and one of the highest values of diversity under the Simpson index (Table 2). *T. amazonia* plantation understories had a higher Shannon–Wiener index, however, indicating that rare species were more prominent in plantations of *T. amazonia* than *V. koschnyi*. Similarly, *V. guatemalensis* had a higher number of total species than *C. brasiliense*, yet *C. brasiliense* ranked higher in both diversity indices. Interestingly, *H. alchorneoides*, which had the fewest number of species, had a relatively high Simpson index of diversity, and a mid-range Shannon–Wiener index.

4.4. Dispersal guilds

Using the SAS General Linear Model, there were no significant differences in species' dispersal mechanisms between the six treatments for all sites. When dispersal mechanism of understory species was compared between sites, La Selva had significantly more species dispersed by bats and birds than the two farmers' plantations. La Selva also had significantly more species dispersed by wind and mammals other than bats than the Paniagua plantations. There were no differences between sites in water or gravity dispersed species. Results from the *k*-means cluster analysis support these findings (Table 3). The Hartigan Rule of Thumb indicated that three clusters (= to the number of sites) were more appropriate than six (= to the number of treatments) for separating plots into groups (the Hartigan ratio should be >10, and was =22 for three clusters, =5 for six clusters).

When individual plots were considered, membership of plots in clusters coincided fairly well with site (Table 3). Cluster 1 was dominated by plots from the Paniagua plantations, Cluster 2 had mostly plots from

Table 3
Membership of plots in *k*-means clusters according to plantation site[a]

Cluster	La Selva (%)	Paniagua (%)	Quesada (%)
1	29	42	29
2	63	17	38
3	8	42	33

[a] See Table 4 for description of clusters.

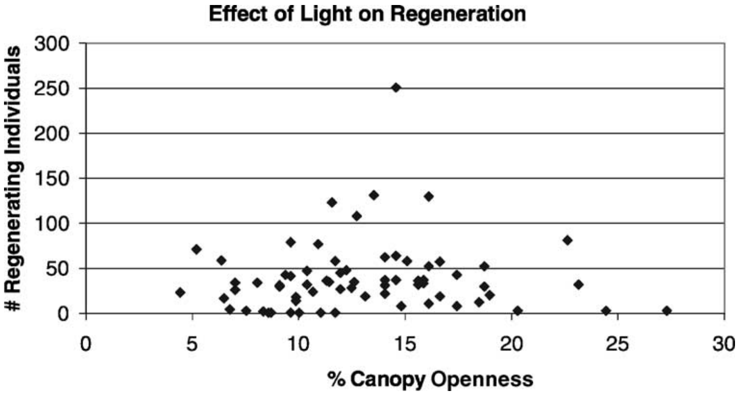

Fig. 5. Number of regenerating individuals in each subplot in relation to canopy openness.

Table 4
Average dispersal mechanism scores for plantation plots assigned to each cluster[a]

Cluster	Mammals	Birds	Wind	Water/gravity	Bats
1	0.92	1.62	0.13	0.00	0.58
2	2.50	4.00	0.61	0.07	0.54
3	0.05	0.20	0.10	0.05	0.15

[a] Averages are based on the number of woody species dispersed by each guild.

La Selva, and Cluster 3 had a fairly even split from the Paniagua and Quesada plantations. Membership in clusters was poorly described by planted timber species, no cluster having more than 30% of its plots from a single timber species. Average dispersal mechanism plot-scores indicated underlying differences between clusters (Table 4). Cluster 1, characterized by Paniagua plots, could be considered a "moderate visitation by birds, bats and mammals" cluster, according to average plot-scores of dispersal mechanism. Cluster 2, characterized by La Selva plots, was a "very high visitation by birds and mammals, moderate influence of bats and wind" cluster. Cluster 3 was a "low visitation" cluster. It was somewhat evenly comprised of plots from the Paniagua and the Quesada plantations (Table 3).

4.5. Effect of canopy openness on understory regeneration

There was no linear correlation between canopy openness and the number of individuals regenerating in individual plots. Using a linear regression, canopy openness explained only 0.1% of understory regeneration abundance. However, a quadratic relationship between canopy openness and understory regeneration was apparent (Fig. 5). Using the SAS General Linear Model to test for polynomial trends, canopy openness had a significant quadratic relationship ($P < 0.02$) with total abundance of regeneration. At low and high levels of canopy openness, woody species were absent in the understory. Using the quadratic model, canopy openness explained 8% of the variability in understory regeneration.

4.6. Effect of plantation floor litter biomass on understory regeneration

There was no linear or quadratic correlation between plantation floor leaf litter biomass, and understory regeneration. Using a linear regression, leaf litter weight explained only 0.3% of understory regeneration abundance. There was, however, a somewhat significant interaction between litter and planted species ($P < 0.07$), and between litter and site ($P < 0.05$). Although planted species was correlated to leaf litter weight, litter weight was not an important factor influencing understory regeneration.

5. Discussion

5.1. Comparison of understory regeneration in plantations

Previous studies of understory regeneration in Costa Rica (Carnevale and Montagnini, 2002; Guariguata et al., 1995; Montagnini, 2000; Powers et al., 1997) and other areas of the tropics (Parrotta et al., 1997) have commonly compared understory regeneration in experimental plantations at a single site. The present research attempted to examine trends across three independent sites planted with the same six timber species. The strongest trend found across all sites, largely corroborated by the above studies, was the success of plantations at recruiting understory regeneration in comparison with abandoned pasturelands ($P < 0.0001$).

Unlike previous studies conducted at a single site, no single timber species among the six studied here emerged as the most successful at recruiting understory regeneration overall (Fig. 1). Results from the experimental plantations at La Selva, nearest to continuous forest and on uniformly flat terrain, did not match results from farmers' plantations with respect to recruitment of natural regeneration. There were also different trends in timber species' success at recruiting understory regeneration between the two farmers' plantations. *C. brasiliense*, *T. amazonia*, and *V. ferruginea* each had the greatest abundance of understory regeneration at one of the three sites. A lack of consistency in understory regeneration across multiple sites was also observed by Haggar et al. (1997) in a study of several 6-year-old plantations in the same region in Costa Rica.

At La Selva, *V. guatemalensis* and *C. brasiliense* had the greatest abundance of understory regeneration, both for total numbers and by height classes. Similarly, in La Selva plantations at 3 years after planting, Guariguata et al. (1995) found that *V. guatemalensis* had higher abundance of woody regeneration than plantations of *Jacaranda copaia*. At 7 years, Montagnini (2001) also found that *V. guatemalensis* had the second highest abundance of regeneration overall at La Selva plantations, after *T. amazonia*. Patterns in regeneration at the La Selva site have clearly changed over time. On other plantations at La Selva, Haggar et al. (1997) also noted changing patterns in regeneration over and 18-month-period. Studies in other regions (Geldenhuys, 1997; Keenan et al., 1997; Loumeto and Huttel, 1997) have demonstrated increased diversity and an increasing proportion of mature forest species regenerating in the understory as timber plantations age. These results, and the changes observed at La Selva, indicate that data from a single survey cannot necessarily predict the future composition of a stand. To fully understand forest succession on plantations, it is necessary to observe long-term changes.

In addition to promoting high diversity of understory regeneration, *V. guatemalensis* has been observed to have high stem biomass increment relative to other native species, and annual stem diameter and volume increments similar to exotic timber species like *Gmelina arborea* (Piotto et al., 2003). In contrast, Piotto et al. (2003) observed that *C. brasiliense* had the lowest mean annual diameter increment among native species plantations in the lowland humid tropics of Costa Rica. Therefore, although *C. brasiliense* had slightly higher understory regeneration, *V. guatemalensis* is a more appropriate species to use for reforestation on sites similar to La Selva.

At the Paniagua plantations *T. amazonia* was the most successful species for total understory regeneration in the three height classes. *T. amazonia* was similarly observed to have the highest abundance of understory regeneration at La Selva in 7-year-old plantations (Montagnini, 2001). Rare species were also an important component of the understory regeneration in *T. amazonia* plots in the present research, as illustrated by the high Shannon–Wiener index. Also, across all sites, *T. amazonia* and *V. guatemalensis* had significantly more regeneration in Height Class 3, possibly indicating greater survivorship of seedlings under these species. Additionally, *T. amazonia* was identified by Piotto et al. (2003) as one of the most promising species for reforestation in the Costa Rican lowland region due to the species' good growth in volume, form, and adaptability to variable site conditions. Therefore, *T. amazonia* is also recommended for reforestation in the region.

At the Quesada plantations, *V. ferruginea* was the most successful species at recruiting understory regeneration overall, and in two of the height classes. Carnevale and Montagnini (2002) recommended *V. ferruginea* for reforestation projects based on the species' good growth, and a high abundance of understory regeneration observed at La Selva in 7-year-old plantations. Despite high abundance of understory regeneration, *V. ferruginea* was found here to have relatively low indices of species diversity. *V. ferruginea* has, however, been observed to improve soil organic matter and soil nutrient content (Montagnini, 2001).

Based on the present research and previous studies, *V. guatemalensis*, *T. amazonia*, and *V. ferruginea* are the most promising species for reforestation projects in areas similar to the Sarapiquí region of Costa Rica. These species were most successful at recruiting understory regeneration, and had overall good growth and timber quality in plantation conditions.

5.2. *Understory composition and dispersal guilds*

As has been found in other studies (Parrotta et al., 1997), the composition of understory regeneration in this study was dominated by a relatively small number of shrub species. While species composition at all sites was dominated by shrub species of the Melastomataceae, Piperaceae, Nyctaginaceae, and Rubiaceae families, there was also considerable regeneration of timber species. Both La Selva and the Quesada plantations had one of the two *Vochysia* timber species among the top five species regenerating in the understory. In 6-year-old plantations at La Selva, Haggar et al. (1997) found that composition in the understory was low in forest tree species. In this study, much of the regenerating *Vochysia* spp. were of the smallest height class, indicating that they might be recent regeneration. *V. koschnyi* was also regenerating from seed and sprout in plots at the Paniagua plantation, though not as abundant as the tree regeneration at the other plantations. Regeneration of timber species was often found in patches, and over 20 individuals of a regenerating timber species were sometimes counted in a single plot. Long-term monitoring of these patches will be necessary to determine survival of timber species regeneration.

The analysis of dispersal guilds showed that clusters of plots were best grouped according to site, rather than overstory species. This result implies that the position of a plantation on the landscape might have a greater influence on seed dispersal than the overstory species. La Selva, closest to continuous forest, had the highest scores for all dispersal guilds, and had much higher bird and mammal dispersal scores than the other sites, using cluster analysis. The Paniagua plantation (characterizing the cluster with intermediate dispersal scores), had lower wind, bird and mammal dispersed species. Bat dispersed species, however, increased slightly for the Paniagua cluster, indicating that bat dispersal was less affected by the moderate distance between plantation and continuous forest (1.3 km) than dispersal by other animals. The final cluster had low scores in all dispersal guilds, and was characterized by plots from the Quesada and Paniagua plantations. The specific plots that were put into this cluster had more open canopies and higher fern growth in their understories. The low dispersal scores of this cluster, therefore, probably reflect unfavorable microhabitat conditions more than seed dispersal.

5.3. *Explanatory factors and understory regeneration*

Canopy openness and plantation floor leaf litter biomass were examined in this study as explanatory factors for differences in understory regeneration. These factors have been shown in other studies to be associated with regeneration of timber species (Ashton et al., 2001; Menalled et al., 1997). Although canopy openness was associated with understory regeneration in this research, there was no significant interaction between canopy openness and planted timber species. This lack of interaction is probably due to the irregularity of thinning regimes applied across sites. It is impossible to conclude from this study, therefore, whether the canopy structure of certain timber species would provide more appropriate light conditions for understory regeneration. Carnevale and Montagnini (2002) did find significant correlations between shading and timber species when studying regeneration under the La Selva plantations at 7 years. The results from the present research demonstrate that the influence of thinning regimes on understory light conditions are important for understory regeneration, and override differences in canopy structure between species.

In this study there was an upper and lower limit of light conditions under which woody regeneration occurred. Other studies have found that very high light conditions are associated with fern or grass dominance in plantation understories (Kuusipalo et al., 1995; Parrotta et al., 1997; Powers et al., 1997). Powers et al. (1997) found that grass and fern cover also explained most of the variance in understory abundance and richness. Similarly, in the present research, plots with the highest incident light generally had understories dominated by ferns, with few or no woody species. Plots with the lowest measurements of incident light generally had a thick leaf litter layer and no woody regeneration.

Despite the lack of correlation between planted species and light, canopy openness was associated with understory regeneration in this study. While Carnevale and Montagnini (2002) found a significant positive correlation between canopy shading and understory regeneration in 7-year-old plantations at La Selva, canopy openness in the present study only explained 8% of the variation in understory regeneration. Among plots with intermediate levels of canopy openness (∼15%), there was high variability in the number of regenerating individuals. Therefore, factors other than light must have been responsible for much of the variance in the understory regeneration in plots with intermediate light conditions. Also, the light conditions when older regeneration established were likely very different from conditions at the time of this survey. For plots with intermediate light, light conditions during this study probably had the greatest influence on recent regeneration.

Unlike previous research, this study found no significant association between leaf litter on the plantation floor and abundance of regeneration. Carnevale and Montagnini (2002) did find increased regeneration in plots with greater litter depth at La Selva. Powers et al. (1997) and Parrotta (1995), in contrast, found litter depth to be negatively correlated with abundance and richness of understory regeneration. Parrotta (1995) suggested that high litter biomass particularly suppresses regeneration of small-seeded (bird-dispersed) species (i.e. most of the shrub species encountered in this study). The contrasting results of the previous studies, and the lack of correlation found in the present research, suggest that the influence of leaf litter on regeneration is highly variable. At least in this study, factors other than leaf litter must have been most important for determining understory regeneration.

5.4. *Influence of site on regeneration*

Why species had variable success at recruiting understory regeneration at the different sites is not completely clear. One explanation for the variation in plantation understory abundance could be the irregularity of planting design and terrain within and between sites. At both farmers' sites, plantations of each timber species were scattered across irregularly undulating terrain (although plots used in this research were chosen randomly). At the two farms, the original plantation design was not systematically randomized with respect to slope and soil characteristics. At La Selva, differences in soil and slope were systematically blocked out in the original experimental design. The thinning regime at La Selva was also probably more precise and more evenly applied than in the two farms.

At the Paniagua plantation, *T. amazonia*, the most successful species at recruiting understory regeneration, was planted on flatter, better drained soils than some of the other species. *T. amazonia* also had an intermediate spacing regime relative to plots of other species at the site. At the Quesada plantation, slope and spacing were more uniform than at the Paniagua plantation. However, plots of *C. brasiliense* and *V. guatemalensis*, which were most successful at La Selva, were uniformly located on sites with poorer drainage than other species at the Quesada plantation. Differences in slope, drainage class, management, irregular thinning, and other site conditions might explain why different timber species were more successful at recruiting understory regeneration at each of the three sites. The sites were not perfect replicates, which might have influenced the variability in results from each site. Further examination of the interaction between planted timber species and specific site factors (such as soil nutrients, drainage and slope), and the impact of this interaction on understory regeneration, could benefit future reforestation projects in the humid lowland tropics.

Acknowledgements

We thank Yehudi Fernández and Corine Vriesendorp for their assistance in identifying plants, and Marisol Luna for field assistance. We also thank FUNDECOR for helping us to identify appropriate plantations, and Vicente Paniagua and Isidro Quesada for allowing us to conduct research in their plantations. Funding was provided by the Tropical Resources Institute at Yale University.

Appendix A

Species list of pooled data from all sites

Family	Species	*C. brasiliense*	*T. amazonia*	*V. guatemalensis*	*H. alchorneoides*	*V. koschnyi*	*V. ferruginea*	Control
Acanthaceae	*Thunbergia* sp. 1	0	0	0	0	2	0	0
Annonaceae	*Annona montana* Macfad.	0	0	1	0	0	0	0
Annonaceae	*Guatteria diospyroides* Baill.	3	3	0	1	0	5	0
Annonaceae	*Rollinia pittieri* Standl.	0	10	5	2	4	3	0
Annonaceae	*Unonopsis pittieri* Saff.	1	0	1	0	0	1	0
Annonaceae	*Unonopsis* sp.	0	0	0	0	2	0	0
Apocynaceae	*Stemmadenia donnell-smithii* (Rose) Woodson	0	0	0	0	2	1	0
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planch.	0	0	2	1	0	0	0
Arecaceae	*Astrocaryum confertum* H. Wendl. ex. Burret	0	0	0	0	1	0	0
Arecaceae	*Iriartea deltoidea* Ruiz & Pav.	0	0	0	0	2	0	0
Arecaceae	*Socratea exorrhiza* (Mart.) H. Wendl.	10	0	2	0	0	0	0
Asteraceae	*Neurolaena lobata* (L.) R. Br.	0	4	0	0	0	0	0
Bignoniaceae	Unknown sp. 1	0	0	0	2	0	0	0
Bignoniaceae	*J. copaia* (Aubl.) D. Don	20	1	0	0	1	3	0
Bignoniaceae	*Mussatia hyacinthina* (Standl.) Sandw.	4	0	0	0	0	0	0
Bignoniaceae	*Tabebuia guayacan* (Seem.) Hemsl.	0	2	0	1	0	0	0
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken	0	0	1	5	0	2	0
Boraginaceae	*Cordia dwyeri* Nowicke	0	0	2	0	0	0	0
Burseraceae	*Protium pittieri* (Rose) Engl.	0	0	0	1	0	0	0
Clusiaceae	*C. brasiliense* Cambess. (seed)	5	1	0	0	0	0	0
Clusiaceae	*Marila laxiflora* Rusby	0	0	0	0	14	0	0
Clusiaceae	*Vismia macrophylla* Kunth	2	8	12	2	1	3	0
Combretaceae	*T. amazonia* (J.F. Gmel.) Exell (resprout)	0	18	0	0	0	0	0
Convolvulaceae	*Ipomoea* sp.	0	0	0	1	3	2	0
Dilleniaceae	*Dilleniaceae* sp.	1	0	0	0	0	0	0
Elaeocarpaceae	*Sloanea* sp.	0	0	0	1	0	0	0
Erythroxylaceae	*Erythroxylum* sp.	0	1	0	0	0	0	0
Euphorbiaceae	*Acalypha diversifolia* Jacq.	0	0	0	0	0	2	0
Euphorbiaceae	*Alchornea costaricensis* Pax & K. Hoffm.	0	2	3	1	1	1	0
Euphorbiaceae	*Croton* sp.	0	2	0	0	0	0	0
Euphorbiaceae	Unknown sp. 1	1	0	0	0	0	0	0
Euphorbiaceae	Unknown sp. 2	0	0	0	0	1	0	0
Euphorbiaceae	*H. alchorneoides* Allemao	0	1	0	2	0	0	0
Euphorbiaceae	*Plukenetia stipellata* L.J. Gillespie	0	0	0	0	2	0	0
Euphorbiaceae	*Plukentia* sp.	0	2	0	0	1	0	0
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	0	0	0	0	0	10	0
Fabaceae/ Caesalpinioideae	*Cassia* sp.	1	0	0	0	0	0	0
Fabaceae/ Caesalpinioideae	*Senna fruticosa* (P. Mill.) Irwin & Berneby	0	0	0	2	0	2	0
Fabaceae/Mimosoideae	*Inga pavoniana* G. Don	0	0	1	0	0	0	0
Fabaceae/Mimosoideae	*Inga thibaudiana* DC.	0	0	0	0	1	0	0
Fabaceae/Mimosoideae	*Inga* sp.	0	1	0	0	8	0	0
Fabaceae/Papilionoideae	*Andira inermis* (Wright) Kunth	2	0	3	0	0	0	0

Appendix A. (*Continued*)

Family	Species	*C. brasiliense*	*T. amazonia*	*V. guatemalensis*	*H. alchorneoides*	*V. koschnyi*	*V. ferruginea*	Control
Fabaceae/Papilionoideae	*Dipteryx panamensis* (Pittier) Record & Mell	0	3	2	1	1	0	0
Fabaceae/Papilionoideae	*Dussia macroprophyllata* (Donn. Sm.) Harms	0	0	1	0	0	1	0
Fabaceae/Papilionoideae	*Pterocarpus officinalis* Jacq.	0	0	0	0	3	0	0
Fabaceae/Papilionoideae	*Pterocarpus rohrii* Vahl	0	0	1	0	1	0	0
Flacourtiaceae	*Carpotroche platyptera* Pittier	0	0	0	0	1	0	0
Flacourtiaceae	*Casearia arborea* (Rich.) Urb.	5	3	1	1	4	2	0
Flacourtiaceae	*Casearia commersoniana* Cambess.	0	1	0	0	0	0	0
Hernandiaceae	*Hernandia didymantha* Donn. Sm.	5	1	3	2	0	4	0
Hernandiaceae	*Hernandia stenura* Standl.	2	1	0	0	3	0	0
Humiriaceae	*Sacoglottis trichogyna* Cuatrec.	2	1	1	0	0	0	0
Lauraceae	*R. kunthiana* (Nees) Rohwer	29	4	35	23	71	14	0
Lauraceae	*Ocotea leucoxylon* (Sw.) Laness	0	0	0	0	1	0	0
Lauraceae	*Ocotea* spp.	3	2	7	5	4	8	0
Malvaceae	*Hampea appendiculata* (Donn. Sm.) Standl.	22	12	17	12	9	3	0
Malvaceae	*Pavonia* sp. 1	0	0	0	0	0	1	0
Melastomataceae	*C. hirta* (L.) D. Don	14	37	45	29	6	16	0
Melastomataceae	*Clidemia* sp.	1	0	0	0	1	0	0
Melastomataceae	*C. subcrustulata*	4	10	4	6	2	0	0
Melastomataceae	*Conostegia* sp.	2	0	0	0	0	1	0
Melastomataceae	Unknown sp. 1	1	0	0	0	0	0	0
Melastomataceae	Unknown sp. 2	1	0	0	0	0	0	0
Melastomataceae	*Miconia* sp. 1	6	10	0	0	28	21	0
Melastomataceae	*Miconia* sp. 2	0	1	5	0	0	0	0
Melastomataceae	*Miconia* sp. 3	0	18	0	1	0	0	0
Melastomataceae	*Miconia affinis* DC.	42	28	11	11	33	2	0
Melastomataceae	*Miconia ellata* (Sw.) DC.	6	2	0	1	0	0	0
Melastomataceae	*Miconia impetiolaris* (Sw.) D. Con ex DC.	0	0	8	1	5	0	0
Melastomataceae	*Miconia longifolia* (Aubl.) DC.	1	15	3	2	2	0	0
Melastomataceae	*Miconia multispicata* Naudin	0	2	1	0	0	0	0
Melastomataceae	*Miconia nervosa* (Sm.) Triana	2	1	2	0	23	0	0
Melastomataceae	*Miconia punctata* (Desr.) D. Don ex DC.	0	2	0	0	0	0	0
Meliaceae	*Carapa* sp.	0	0	0	0	1	0	0
Meliaceae	*Cedrela odorata* L.	0	0	1	0	0	1	0
Meliaceae	*Guarea guidonia* (L.) Sleumer	0	0	0	0	1	0	0
Meliaceae	*Guarea* sp.	0	0	3	0	1	0	0
Mimosoideae	*Pentaclethra macroloba* (Willd.) Kuntze	23	5	0	0	13	0	0
Monimiaceae	*Siparuna* sp.	0	2	2	0	0	3	0
Moraceae	*Castilla elastica* Sesse	0	0	1	0	1	2	0
Moraceae	*Cecropia insignis* Liebm.	0	1	0	0	0	3	0
Moraceae	*Cecropia obtusifolia* Bertol.	0	2	2	1	0	0	0
Moraceae	*Cecropia peltata*	0	0	0	0	0	1	0
Moraceae	*Ficus* sp.	1	1	9	4	0	3	0
Moraceae	*Pourouma bicolor* Mart.	0	0	0	1	0	0	0
Moraceae	*Pourouma minor* Benoist	0	0	0	0	6	0	0
Moraceae	*Sorocea pubivena* Hemsl.	0	0	0	0	1	0	0
Moraceae	*Trophis involucrata* W.C. Burger	1	0	1	1	0	1	0
Myristicaceae	*V. koschnyi* Warb.	3	3	8	3	11	7	0

Appendix A. (*Continued*)

Family	Species	*C. brasiliense*	*T. amazonia*	*V. guatemalensis*	*H. alchorneoides*	*V. koschnyi*	*V. ferruginea*	Control
Myrtaceae	*Eugenia* sp.	1	0	0	0	0	0	0
Myrtaceae	Unknown sp. 1	5	0	0	0	0	0	0
Nyctaginaceae	*N. psychotrioides* Donn. Sm.	78	36	142	34	20	23	0
Passifloraceae	*Passiflora* sp.	0	0	0	4	7	0	0
Piperaceae	*Piper* spp.	33	75	72	49	72	59	0
Rhizophoraceae	*Cassipourea elliptica* (Sw.) Poir.	1	0	0	0	0	0	0
Rubiaceae	*Bertiera guianensis* Aubl.	0	0	1	0	0	0	0
Rubiaceae	*Hamelia patens* Jacq.	0	0	0	1	0	0	0
Rubiaceae	*Palicourea guianensis* Aubl.	19	3	7	17	7	20	0
Rubiaceae	*Pentagonia donnell-smithii* (Standl.) Standl.	1	12	3	2	4	1	0
Rubiaceae	*Psychotria elata* (Sw.) Hammel	32	6	36	20	15	14	0
Rubiaceae	*Psychotria luxurians* Rusby	2	1	3	0	0	0	0
Rubiaceae	*Psychotria panamensis* Standl.	10	0	2	0	2	0	0
Rubiaceae	*Psychotria suerrensis* Donn. Sm.	2	0	3	0	5	1	0
Rubiaceae	*Psychotria* spp.	1	3	0	2	2	0	0
Rubiaceae	*S. panamensis*	17	11	2	3	8	2	0
Rubiaceae	*Sabicea* sp.	0	4	5	0	0	0	0
Rubiaceae	*Uncaria* sp.	0	0	0	0	7	0	0
Rutaceae	*Zanthoxylum panamense* P. Wilson	0	0	0	0	0	4	0
Sapindaceae	*Cupania pseudostipularis* T.D. Penn.	0	0	0	0	1	0	0
Sapindaceae	*Paullinia* sp.	0	0	1	0	0	0	0
Simaroubaceae	*Simarouba amara* Aubl.	15	0	0	6	2	2	0
Solanaceae	*Cestrum racemosum* Dunal	0	0	0	0	2	0	0
Solanaceae	*Cestrum* sp.	0	0	1	0	0	0	0
Solanaceae	*Cestrum racemosum* Ruiz & Pav.	0	0	1	0	0	0	0
Solanaceae	*Cestrum* sp.	2	3	1	2	0	1	0
Solanaceae	*Cuatresia cuneata* (Standl.)	0	0	0	13	0	0	0
Solanaceae	*Solanum* spp.	5	1	0	0	4	0	0
Solanaceae	*Witheringia* spp.	6	2	8	0	5	4	0
Tiliaceae	*Goethalsia meiantha* (Donn. Sm.) Burret	0	0	0	0	0	1	0
Unknown	Unknown 1	0	1	1	0	0	0	0
Unknown	Unknown 2	0	0	0	1	0	0	0
Unknown	Unknown 3	2	0	0	0	0	0	0
Unknown	Unknown liana 1	0	2	0	0	0	0	0
Urticaceae	*Urera* sp.	0	0	0	2	0	0	0
Verbenaceae	*Vitex cooperi* Standl.	4	0	1	2	0	4	0
Vernonieae	*Piptocarpha chotalense*	0	4	0	2	0	2	0
Vernonieae	*Piptocarpha poeppigiana* (DC.) Baker	0	0	0	0	1	0	0
Vernonieae	*Piptocarpha* sp.	0	0	0	0	0	1	0
Violaceae	*Gloeospermum boreale* C.V. Morton	0	1	0	0	0	0	0
Vitaceae	*Cissus microcarpa* Vahl	0	0	0	0	1	0	0
Vochysiaceae	*V. guatemalensis* Don. Sm	80	4	106	1	0	2	0
Vochysiaceae	*V. ferrugineae* Mart. (seed)	0	0	0	0	0	103	0
Vochysiaceae	*V. ferrugineae* Mart. (resprout)	0	0	0	0	0	1	0
Total		542	393	603	288	444	374	0

References

Ashton, M., Gunatilleke, C., Singhakumara, B., Gunatilleke, I., 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. For. Ecol. Manage. 525, 1–23.

Carnevale, N., Montagnini, F., 2002. Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species. For. Ecol. Manage. 163, 217–227.

FAO (Food and Agricultural Organization of the United Nations), 2000. http://www.fao.org/forestry.

Geldenhuys, C.J., 1997. Native forest regeneration in pine and eucalypt plantations in Northern Province, South Africa. For. Ecol. Manage. 99, 101–115.

Grubb, P.J., 1995. Mineral nutrients and soil fertility in tropical rainforests. In: Lugo, A.E., Lowe, C. (Eds.), Tropical Forests: Management and Ecology. Springer, New York, pp. 308–330.

Guariguata, M., Rheingans, R., Montagnini, F., 1995. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. Restor. Ecol. 3, 52–260.

Haggar, J., Wightman, K., Fisher, R., 1997. The potential of plantations to foster woody regeneration within a deforested landscape in lowland Costa Rica. For. Ecol. Manage. 99, 55–64.

Keenan, R., Lamb, D., Woldring, O., Irvine, T., Jensen, R., 1997. Restoration of plant biodiversity beneath tropical tree plantations in northern Australia. For. Ecol. Manage. 99, 117–131.

Keenan, R., Lamb, K., Parrotta, J., Kikkawa, J., 1999. Ecosystem management in tropical timber plantations: satisfying economic, conservation, and social objectives. J. Sustain. For. 9, 117–134.

Kuusipalo, J., Goran, A., Jafarsidik, Y., Otsamo, A., Tuomela, K., Vuokko, R., 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: understory development in forest plantations. J. Veg. Sci. 6, 205–210.

Loumeto, J.J., Huttel, C., 1997. Understory vegetation in fast-growing tree plantations on savanna soils in Congo. For. Ecol. Manage. 99, 65–81.

Lugo, A.E., 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. For. Ecol. Manage. 99, 9–19.

Menalled, F., Kelty, M., Ewel, J., 1997. Canopy development in tropical tree plantations: a comparison of species mixtures and monocultures. For. Ecol. Manage. 104, 249–263.

Montagnini, F., 2000. Strategies for the recovery of biodiversity in deforested landscapes. In: Krishnapullay, B., Soepadmo, E., Arshad, M., Wong, A., Appanah, S., Wan Chik, S., Manokaran, N., Tong, H., Choon, K. (Eds.), Forests and Society: The Role of Research. IUFRO World Congress, August 6–12, 2000. Subplenary Sessions, vol. 1. International Union of Forestry Research Organizations, Kuala Lumpur, Malaysia, pp. 310–319.

Montagnini, F., 2001. Strategies for the recovery of degraded ecosystems: experiences from Latin America. Interciencia 26, 498–503.

Parrotta, J., 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. Agric. Ecosyst. Environ. 41, 115–133.

Parrotta, J., 1995. Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. J. Veg. Sci. 6, 627–636.

Parrotta, J., Turnbull, J., Jones, N., 1997. Catalyzing native forest regeneration on degraded tropical lands. For. Ecol. Manage. 99, 1–7.

Piotto, D., Montagnini, F., Ugalde, L., Kanninen, M., 2003. Performance of forest plantations in small- and medium-sized farms in the Atlantic lowlands of Costa Rica. For. Ecol. Manage. 175, 195–204.

Powers, J.S., Haggar, J.P., Fisher, R.F., 1997. The effect of overstory composition on understory woody regeneration and species richness in seven year old plantations in Costa Rica. For. Ecol. Manage. 99, 43–54.