Forest Ecology and Management 163 (2002) 217–227

Forest Ecology and Management

www.elsevier.com/locate/foreco

Facilitating regeneration of secondary forests with the use of mixed and pure plantations of indigenous tree species

Nélida J. Carnevale[a], Florencia Montagnini[b,*]

[a]Faculty of Agricultural Sciences, National University of Rosario, C.C. 14 (S2125-ZAA) Zavalla, Santa Fe, Argentina
[b]Management and Conservation of Forests and Biodiversity, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), 7170 Turrialba, Costa Rica

Received 27 December 2000; accepted 28 April 2001

Abstract

The establishment of tree plantations on degraded lands can facilitate the regeneration of native species that could not otherwise grow in open micro sites or in competition by herbaceous species. The present research investigated tree regeneration under mixed and pure plantations of native species at La Selva Biological Station in the Atlantic humid lowlands of Costa Rica. The highest abundance of regenerating tree individuals was found in the understory of the mixed plantation (composed of *Hieronyma alchorneoides* + *Vochysia ferruginea* + *Balizia elegans* + *Genipa americana*) with 10,156 individuals/ha, followed by pure plantation of *H. alchorneoides* with 7891, *V. ferruginea* with 5703, *B. elegans* with 4219, *G. americana* with 1484, and the natural regeneration control with 703 individuals/ha. The highest mean number of species was found in the understory of the mixed plantation (11 species in 32 m^2), followed by pure plantation of *V. ferruginea* (8.0), *H. alchorneoides* (7.0), *B. elegans* (5.0), *G. americana* (3.0) and control (1.0).

Melastomataceae was the most abundant family in the understory of the mixed plantation and in the pure plantation of *V. ferruginea*, while Rubiaceae was the most abundant under *H. alchorneoides*. In constrast, Piperaceae was the most abundant family under pure plantations of *G. americana* and *B. elegans*. In addition, species of primary forest of the region were found in the understory of the mixed plantation and under the pure plantations of *H. alchorneoides* and *V. ferruginea*. These are promising indicators for the use of these plantations as accelerators of natural forest succession in the region. Very few woody species were found in the control, natural regeneration plots. Factors that may impede the establishment of woody species in the control may be the lack of perches for seed dipersers and invasion by herbaceous vegetation which outcompetes the tree seedlings in their growth.

Keywords: Competition; Dispersers; Litter; Mixed plantations; Regeneration; Shade

1. Introduction

The principal factors limiting tree regeneration in abandoned pastures in tropical humid regions can include scarcity of nutrients, soil compaction, lack or excess of soil humidity, high solar radiation, and intra- and inter-specific competition (Nepstad et al., 1991). Another limiting factor is seed availability, especially in sites whose distance to seed sources may limit propagule dispersal. Several tree species exist in low densities in the natural forests surrounding the pastures, diminishing the possibilities of dispersal of these species. Although the presence of perches favors seed dispersal, other factors such as seed

* Corresponding author. Present address: School of Forestry and Environmental Studies, Yale University, 370 Propect St., New Haven, CT 06511, USA.

0378-1127/02/$ – see front matter
PII: S0378-1127(01)00581-3

predation may limit seed survival and germination in abandoned pastures (Mc Clanahan and Wolfe, 1993; Holl, 1998). Trampling by cattle may be a main factor leading to the elimination of seedlings growing in pastures (Harvey and Haber, 1999).

The presence of trees, either in plantation, in groups, in lines or in isolated form may contribute to the recovery of environmental conditions favorable to tree regeneration processes (Parrotta, 1995; Guariguata et al., 1995). For example, in pasture sites in Monteverde, Costa Rica, seedlings of primary forest species were observed under the canopy of isolated trees, suggesting that seeds can germinate under the shade of parental trees (Harvey and Haber, 1999). In other research in southern Costa Rica, germination of seeds of tree species dispersed in pastures was similar to that in forests, although germination rates were considerably lower in the pasture during the dry season (Holl, 1999).

The establishment of tree plantations in degraded areas may facilitate regeneration of native species that could not otherwise establish in open microsites or in competition by herbaceous species (Lugo, 1992). Several authors report on the role of tree plantations as catalizers of natural succession in tropical and subtropical sites (Parrotta, 1992, 1995; Jussi et al., 1995; Parrotta et al., 1997; Keenan et al., 1999; Parrotta, 1999; Otsamo, 2000). For example, in southeast Asia, Jussi et al. (1995) reported on the spontaneous and fast growth of indigenous tree species under plantations of exotic trees. On the other hand, in north Queensland, Australia, a greater diversity of species was found in the understory of plantations of native species than in plantations of exotic species (Keenan et al., 1999). In Puerto Rico, in the understory of plantations of *Albizia lebbek*, 22 species of trees and shrubs were found, in comparison with just one species in control plots without trees (Parrotta, 1992). At La Selva Biological Station, Costa Rica, results of some studies also suggest that tree plantations have a good potential for accelerating the processes leading to recovery of biodiversity in degraded soils (Guariguata et al., 1995; Powers et al., 1997; Montagnini et al., 1999). On the other hand, high establishment and maintenance costs are potential disadvantages of the use of plantations for accelerating natural regeneration, given the intensive management that is needed especially on the first 2–3 years (Montagnini et al., 1995).

Mixed plantations could promote the regeneration of a greater diversity of species in their understory than pure-species plantations by creating a greater variability of habitat conditions that may favor seed dispersers and germination and growth of tree species (Guariguata et al., 1995; Montagnini et al., 1999). In the present research we investigated tree regeneration under plantations of native species in pure and mixed designs, at La Selva Biological Station in the Atlantic humid lowlands of Costa Rica. In previous research with other species in pure and mixed plantations, also at La Selva, tree regeneration was more successful under the forest plantations than in abandoned pastures (Guariguata et al., 1995; Montagnini et al., 1999). In the present research the following hypotheses were tested. (1) Tree regeneration of native species is more abundant under the canopy of the plantations than in adjacent areas without trees (control); (2) tree regeneration is more diverse under the mixed plantations than under the pure-species plantations; (3) tree regeneration is greater under the plantation species whose litter decomposes more rapidly, because nutrients released from decomposition will favor seedling growth; (4) tree regeneration is less abundant in areas with higher litter accumulation, since this may impede seed germination or seedling growth; and (5) the majority of the tree species regenerating in the understory of plantations are animal-dispersed.

2. Methods

2.1. Site description

The plantations were at La Selva Biological Station, Costa Rica (10°26′N, 86°59′W, 50 m mean altitude, 24 °C mean annual temperature, 4000 mm mean annual rainfall). Soils are Fluventic Dystropepts derived from volcanic alluvium. They are deep, well drained, stone-free, acid (pH in water <5.0), with low or medium organic matter prior to planting (2.5–4.5%), cation exchange capacity 10–14 mol/kg, 10–15% base saturation, and moderately heavy texture (50–60% sand, 5–15% silt and 25–45% clay) (Sancho and Mata, 1987). Prior to plantation establishment, soil conditions were too poor for cultivation of bananas or other commercial crops commonly grown in the region (Bertsch, 1986; Sancho and Mata, 1987; Montagnini, 1994).

The experimental plantations were part of a larger project to compare growth and nutrient dynamics in mixed and pure stands with indigenous tree species (Montagnini et al., 1995). The plantations were established on land that was cleared in the mid-1950s, grazed until 1981, then abandoned. In 1990, at the time of clearing for the plantations, the site was covered with shrubs and early successional trees, interspersed with patches of grass and ferns. The experimental site was surrounded by 15–18 year old secondary forest, and primary forest of La Selva reserve was about 1000 m distance from the site. For the purposes of this research, the site was cleared manually and the slash was left on the floor to protect against soil erosion and to delay the growth of weeds. Planting date was November 1992; the plantations were 7 years old when this research was conducted.

Species selection for the plantations was based upon good growth (González and Fisher, 1994; González et al., 1990), economic value, and seedling availability. The species of this research were *Vochysia ferruginea* Mart. (Vochysiaceae), *Hieronyma alchorneoides* Fr. Allemao (Euphorbiaceae), *Balizia elegans* (Ducke) Barneby and Grimes (Fabaceae, subfamily Mimosoideae) and *Genipa americana* L. (Rubiaceae). *H. alchorneoides* and *V. ferruginea* are good timber species and their seeds and seedlings are commercially available. *B. elegans* was chosen because it is a nitrogen-fixing species. Although they are not planted by farmers, previous research had suggested that *B. elegans* and *G. americana* were promising species for reforestation.

Plantation plots were in randomized blocks, with four replicates of six treatments: pure plantation plots of each species, mixed-species plots (with all four species), and plots that were not planted and left for natural forest regeneration as control. Each plantation plot was 32 m × 32 m. Initial planting distance was relatively tight (2 m × 2 m) to speed canopy closure and obtain early impacts on soils. The three plantations were thinned at 3 and 6 years after planting. With thinning, the initial 2 m × 2 m planting distance (2500 trees/ha) was widened to 2 m × 4 m and then to 4 m × 4 m. Within each mixed-tree plot, trees of the four species were planted with two species per row. Within each row the different species were planted alternately. The sequential order of the species within rows was systematically reversed every other row (Montagnini et al., 1995). The experimental plots were weeded manually as needed and no herbicides were used. Table 1 shows data on height, diameter at breast height (DBH) and basal area of the plantation from measurements taken at 70 months of age (Montagnini and Ugalde, in preparation).

2.2. Tree regeneration studies

Methods used in this research are similar to those used in previous studies done in other two plantations at La Selva (Guariguata et al., 1995; Montagnini et al., 1999). Two 4 m × 4 m subplots were randomly located in each plantation plot, discarding borders. Total sampling area was 32 m^2 for each plot. In each subplot, all woody seedlings and saplings were identified and counted, and were sorted by height classes: class 1: 15 cm–1 m, class 2: 1.05–2 m, class 3: >2.0 m. Similar sampling procedures were used in the adjacent natural regeneration controls. Species

Table 1
DBH, height and basal area of plantations at La Selva Biological Station, from measurements taken at 70 months of age[a]

Plantation	DBH (cm)	Total height (m)	Basal area (m^2/ha)	No. of trees/ha
V. ferruginea	17.5	12.8	21.1	863
H. alchorneoides	13.0	13.6	11.9	893
B. elegans	12.0	9.9	16.6	1473
G. americana	10.6	9.0	7.7	907
Mixed plantation	13.3	11.4	13.9	1011

[a] All values are means of four replicate plots. The measurements for the mixture are averages of the four species present in the mixed stands.

identification was done at the herbarium of La Selva Biological Station. The modes of dispersal of the species were found in the literature.

2.3. Canopy shading and depth of the litter layer

A scale suggested by Powers et al. (1997) was used to relate natural regeneration with canopy shading in the plantation understory and in the natural regeneration controls. This scale uses values from 1 to 4, according to a visual estimation of the specific microsite under consideration, (1) full direct light; (2) diffuse light; (3) lateral light; (4) full shade.

For measuring the depth of the litter layer, four points were randomly located in each subplot, and depth of the litter layer was measured with a ruler to 1 mm. Data on litter decomposition and accumulation were obtained from Horn and Montagnini (1999).

2.4. Data analyses

One-way analysis of variance (ANOVA) was used to compare abundance of regenerating individuals among the different treatments, for each height class and for the totals (sum of the individuals in the three height classes). ANOVA was also used to compare the total number of tree species regenerating under each treatment, canopy shading and depth of the litter layer. L.S.D. tests were used for comparisons among means (Scheffe, 1959).

Shannon diversity indices (H) (Shannon, 1948) were calculated for all treatments. Pearson coefficients were used to correlate the number of individuals and the number of species with canopy shading, using the quantitative scale proposed by Powers et al. (1997) as shown in the previous section. Correlations were also run among numbers of individuals and depth of the litter layer, and among numbers of species and depth of litter layer, also using Pearson coefficient.

3. Results

3.1. Regeneration of woody species under each treatment

3.1.1. Abundance

The highest average of total numbers of tree individuals (seedlings and saplings, sum of the three height classes) was found in the mixed plantation with 10,156 individuals/ha, followed by the pure plantations of *H. alchorneoides* with 7891, *V. ferruginea* with 5703, *B. elegans* with 4219, *G. americana* with 1484 and the control natural regeneration plots with only 703 individuals/ha (Table 2). These differences were statistically significant ($P < 0.00001$), except among *B. elegans* and *V. ferruginea*, and among *B. elegans* and *G. americana* plantations (Table 2).

Sorting the regenerating individuals by height classes, in class 1: 15 cm–1 m the highest numbers of seedlings were found under the mixed plantation, followed by *V. ferruginea*, *B. elegans, H. alchorneoides* and *G. americana*, and none in the control (Fig. 1). Differences among the mixed plantation and *B. elegans*, and among *V. ferruginea* and *G. americana* were statistically significant ($P < 0.0133$).

The highest number of tree regenerating individuals corresponding to height class 2: 1.05–2 m, was also

Table 2
Abundance of regenerating individuals, number of species, canopy shading index and litter depth under pure and mixed plantations, and in natural regeneration plots (means and standard errors between parenthesis)[a]

Treatment	Total number of seedlings/saplings/ha	No. of species/32 m^2	Canopy shading index	Litter depth (cm)
V. ferruginea	5703 (1046) bc	8.25 (0.62) ab	3.62 (0.23) a	7.76 (0.56) a
H. alchorneoides	7891 (712) ab	7.25 (0.75) b	2.62 (0.37) b	6.84 (1.02) a
B. elegans	4219 (1053) cd	5 (0.40) bc	1.87 (0.23) c	1.25 (0.62) b
G. americana	1489 (725) de	3.25 (1.70) cd	1.12 (0.12) d	0.88 (0.51) b
Mixed	10156 (1494) a	11.25 (1.88) a	3 (0) ab	6.38 (1.24) a
Natural regeneration	702 (703) e	0.75 (0.75) d	1 (0) d	0.00 (0) b

[a] Differences among means are statistically significant when the standard error is followed by different letters ($N = 4$, $P < 0.05$).

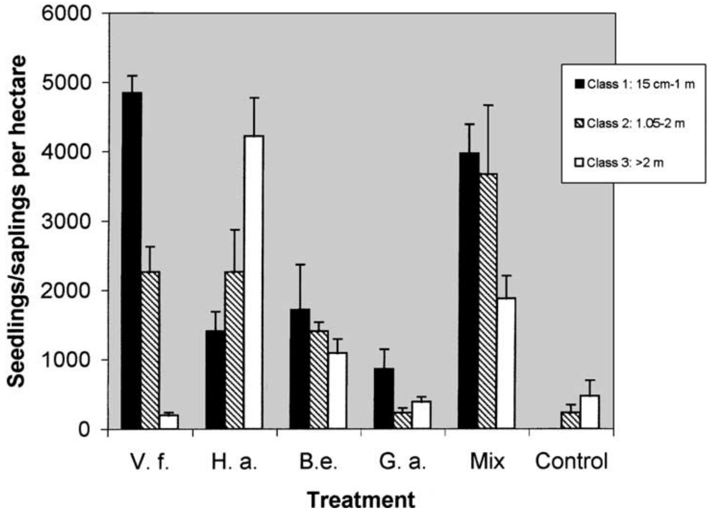

Fig. 1. Total number of regenerating tree seedlings and saplings by height class and treatment. V.f: *V. ferruginea*; H.a.: *H. alchorneoides*; B.e.: *B. elegans*; G.a.: *G. americana*; Mix: mixed plantation; Control: natural regeneration plots.

found under the mixed plantation, followed by *V. ferruginea* and *H. alchorneoides*, and with significantly lower means, *B. elegans*, *G. americana* and natural regeneration control plots (Fig. 1). Differences between the mixed plantation and *B. elegans*, between the mixed plantation and *G. americana*, and between the mixed plantation and the natural regeneration control were statistically significant ($P < 0.0266$).

In height class 3 (> 2 m) the highest number of tree individuals was found under *H. alchorneoides* (Fig. 1). This value was significantly different from all other values ($P < 0.001$).

3.1.2. Number of tree species

The highest number of tree species was found under the mixed plantation (11.2 species in 32 m^2), followed by *V. ferruginea* (8.2), *H. alchorneoides* (7.2), *B. elegans* (5.0), *G. americana* (3.2) and the natural regeneration control (0.7) (Tables 2 and 3). There were statistically significant differences ($P < 0.0001$) among the mixed plantation and *B. elegans*, among *B. elegans* and the natural regeneration control and among *V. ferruginea* and *G. americana* (Table 2).

The highest diversity index was found in the mixed plantation (1.93) and *V. ferruginea* (1.82), followed by *H. alchorneoides* (1.63), *B. elegans* (1.45), *G. americana* (0.89) and the control (0.01).

3.2. Canopy shading and depth of litter layer

The lowest degree of canopy shading was found in the control plots (natural regeneration) (1.0), followed by *G. americana* (1.12), *B. elegans* (1.87), *H. alchorneoides* (2.62), mixed plantation (3) and *V. ferruginea* (3.62). Differences among treatments were statistically significant ($P < 0.00001$), except for the differences among *V. ferruginea* and the mixed plantation, and among the mixed plantation and *H. alchorneoides* (Table 2).

Values of depth of the litter layer were the following (in decreasing order): *V. ferruginea* (7.76 cm), *H. alchorneoides* (6.84 cm), mixed plantation (6.38 cm), *B. elegans* (1.25 cm), *G. americana* (0.88 cm) and natural regeneration with 0 cm. Differences among the mixed plantation, *H. alchorneoides* and *V. ferruginea* versus *B. elegans*, *G. americana* and natural regeneration were statistically significant ($P < 0.00001$) (Table 2).

3.3. Correlation among the abundance of tree regeneration and shading and litter depth

The correlation coefficient between the total number of individuals and the degree of canopy shading was 0.72. The correlation coefficient between

Table 3
Number of tree individuals of each species, regenerating under the mixed plantation (*Hieronyma alchorneoides* + *Vochysia ferruginea* + *Balizia elegans* + *Genipa americana*), under pure plantations of *Vochysia ferruginea*, *Hieronyma alchorneoides*, *Genipa americana* and *Balizia elegans*, and in the natural regeneration control

Species	Mixed plantation	*Vochysia ferruginea*	*Hieronyma alchorneoides*	*Genipa americana*	*Balizia elegans*	Control
Miconia affinis	20	8	7	3	7	3
Neea psychotroides	20	2	0	0	1	0
Nectandra sp.	13	5	0	0	1	0
Piper colonense	16	0	3	5	21	0
Hampea appendiculata	8	1	1	0	0	0
Psychotria panamensis	8	7	16	0	8	0
Psychotria brachiata	6	7	7	1	0	5
Stryphnodendron microstachyum	4	1	0	0	0	0
Simarouba amara	3	4	1	0	0	0
Dypterix panamensis	3	1	0	0	0	0
Clidemia dentata	2	0	0	1	5	0
Cephalis sp.	2	0	0	0	0	0
Rollinia pittieri	2	1	0	0	0	0
Hernandia sp.	2	2	0	0	0	0
Piper sancti-felicis	2	0	1	0	3	0
Miconia elata	2	0	0	0	0	0
Piper aereanum	1	0	0	0	0	0
Pentagonia donnall smithii	1	1	0	0	0	0
Stegmadenea donnall smithii	1	0	0	0	0	0
Miconia serrulata	1	0	0	0	0	0
Casearia arborea	1	2	0	0	0	0
Balizia elegans	1	0	0	0	0	0
Pentaclethra macroloba	1	2	6	0	3	0
Unknown1	1	1	1	0	0	0
Piper trigonium	0	5	0	3	2	0
Nectandra membranaceae	0	3	0	0	0	0
Dendropanax arboreus	0	3	0	0	0	0
Jacaranda copaia	0	3	0	0	0	0
Siparuna pauciflora	0	1	0	0	0	0
Miconia nervosa	0	1	0	0	0	0
Palicourea guianensis	0	0	2	0	0	0
Abarema macrodemia	0	0	1	0	0	0
Cordia alliodora	0	0	1	0	0	0
Ocotea babosa	0	0	1	0	0	0
Unknown 2	0	0	1	0	0	0
Conostegia subcrustulata	0	0	0	2	1	0
Cecropia obtusifolia	0	0	0	1	0	1
Cuatresia cuneata	0	0	0	1	0	0
Solanum rugosum	0	0	0	1	1	0
Urea cavacasana	0	0	0	1	0	0
Cecropia brasiliense	0	0	0	0	1	0
Total	121	61	49	19	54	9

the number of species and the degree of canopy shading was 0.74.

The correlation coefficient between the total number of individuals and the litter depth was 0.69. The correlation coefficient between the number of species and the litter depth was 0.65.

3.4. Principal tree species and families in the six treatments

In the mixed plantation (Table 3), *Miconia affinis* (Melastomataceae) and *Neea psychotroides* (Nyctaginaceae) each represented 16.5% of the total regenerating individuals. The Lauraceae family (*Nectandra* spp.) was third with 10.7% of the total. The mixed plantation had the highest number of species (24) followed by the pure plantation of *V. ferruginea* (21), *H. alchorneoides* (14), *B. elegans* (12), *G. americana* (10), and the control with only three different species (Table 3). Although *B. elegans* only had 12 different species, it had higher abundance of individuals than either *H. alchorneoides*, *G. americana* or the control. Although both the mixed plantation and *V. ferruginea* had the highest diversity indices, it can be seen in Table 3 that the mixed plantation had the highest floristic richness of all treatments.

In the *V. ferruginea* plantation (Table 3) *Miconia affinis*, in the Melastomataceae family, was dominant with 13.3%. The Rubiaceae family (*Psychotria brachiata* and *Psychotria panamensis*), followed in second and third place. In the *H. alchorneoides* plantation the Rubiaceae family was first and second place (Table 3) with a total of 46.3%; the Melastomataceae family was third, with the most frequent species in this plantation, *M. affinis*, making a 14.3% of the total. In the *G. americana* plantation (Table 6) two species of the Piperaceae family (*Piper colonense, Piper trigonium*) were first and second in the proportion of regenerating individuals (42.1%). *M. affinis* was third with 15.8%. In the *B. elegans* plantation (Table 3) members of the Piperaceae family were first with 38.8% of the total, followed by *P. panamensis* in the Rubiaceae family with 14.8%, and *M. affinis* with 12.9%. In the natural regeneration control (Table 3) there were individuals of the Rubiaceae family (55.5%), Melastomataceae (33.3%) and Cecropiaceae (11.1%).

4. Discussion

4.1. Tree regeneration in mixed and pure plantation: seedling abundance and species richness

The results of this research confirm the first hypothesis, that tree regeneration was more abundant in the understory of the plantations that in areas free of trees. This coincides with results of other published research on the subject (Parrotta, 1992; Mc Clanahan and Wolfe, 1993; Guariguata et al., 1995; Powers et al,. 1997; Holl, 1999; Parrotta, 1999; Keenan et al., 1999; Montagnini et al., 1999).

The second hypothesis of this research, that tree regeneration was more diverse under the mixed plantation than under the pure species plantations, was also confirmed, since the mixed plantation had the highest number of species and highest diversity index. In previous research with other pure and mixed plantations at La Selva, mixed plantations had the highest abundance of tree individuals in their understory, along with the pure plantations of *Vochysia guatemalensis* and *Calophyllum brasiliense*, and they were second to *V. guatemalensis* in number of species (Chávez, 1998). In other research also at La Selva, the mixed plantations were second to *Terminalia amazonia* plantations in terms of tree seedling abundance, and had the highest numbers of tree seedling species along with the pure plantations of *T. amazonia, Virola koschnyi,* and *Dipteryx panamensis* (Ribeiro, 1998). In similar studies carried on in Puerto Rico, Parrotta (1999) reported that there were no statistically significant differences in abundance of tree seedlings among pure plantations of *Leucaena* and mixed plantations of *Leucaena/Casuarina*; and that the regeneration density was higher in the pure plantations of *Casuarina* than in the pure plots of *Eucalyptus* or in the mixed plots of *Eucalyptus/Casuarina*. However, for the same site it was found that species richness was higher in the mixed plantations of *Eucalyptus/Casuarina* than in the pure *Casuarina* plantations (Parrotta, 1999). Apparently, in some cases species richness was greater in mixed than in pure plantation, even if abundance was similar between the two plantation types.

The presence of a greater proportion of individuals of height class 1: 15 cm–1 m in the understories of the mixed plantation and in the *V. ferruginea* plantation suggests that the relatively high shading conditions and medium to high litter depth in these treatments are favorable for arrival and germination (recruitment) of tree seeds. Likewise, for height class 2 (1.05–2 m) the most favorable conditions were in the mixed plantation. However, for individuals of height class 3 (>2 m) the greatest numbers of tree seedlings were found under the *H. alchorneoides* pure plantations. This suggests that although recruitment was most favored in the mixed and in the *V. ferruginea* plantations, seedling survival was higher in *H. alchorneoides*.

In *H. alchorneoides* plantations, canopy shading and litter depth were one of the highest, suggesting that these conditions may favor seedling survival and growth.

Pure plantations of *V. ferruginea* ranked second to the mixed plantations in terms of numbers of tree species regenerating in the understory. This result agrees with the findings reported by Powers et al. (1997), who examined natural regeneration in the understory of eight plantation species and a natural regeneration control, also at La Selva. These authors found that plantations of *V. guatemalensis* and *V. ferruginea* contributed to early supression of grass and attracted a large amount of seed dispersers. Likewise, Guariguata et al. (1995), reported that in *V. guatemalensis* plantations at La Selva there was a higher diversity of life forms growing in the understory. Apparently, both species of *Vochysia, V. guatemalensis* and *V. ferruginea*, provide favorable conditions for regeneration of tree species under their canopies, both in terms of density and species richness. It is interesting to note that these two species are preferred for reforestation in the region because of their good growth (Table 1) and high timber value (González and Chaves, 1994; Montagnini et al., 1995). In addition, improvements in soil organic matter and fertility conditions have been reported under *V. ferruginea*, in comparison with other plantation species or pastures (Montagnini and Sancho, 1990; Stanley and Montagnini, 1999).

The results of the correlation analyses suggest that the degree of canopy shading and litter depth were factors influencing numbers of individuals and species richness, with canopy shading probably having a greater influence on tree regeneration than litter depth. The third hypothesis of this research, which stated that tree regeneration was greater in the sites with fastest litter decomposition, the pure plantations of *B. elegans* and *G. americana* (Horn and Montagnini, 1999) was not confirmed. On the contrary, in these plantations the density of regenerating seedlings was less than in all other plantation treatments, probably due to higher illumination and greater density of herbaceous vegetation under these species. The implicit hypothesis, stating that tree regeneration was less abundant in the sites with less litter depth, consequently was not confirmed either. *V. ferruginea* and *H. alchorneoides* had one of the largest abundance of regenerating tree seedlings under their canopies, and they also had the largest annual accumulation of litter on the floor (Horn and Montagnini, 1999). This coincides with results from research on eight plantation species at La Selva by Montagnini et al. (1999), who found that tree regeneration was larger under the plantation species whose amount of annual litterfall and litter accumulation were the most abundant. High production and accumulation of litter contribute to inhibit growth of herbaceous species, thus favoring establishment by tree species. Apparently, in this site the suppresion of herbaceous species was more important as a factor favoring natural regeneration than nutrients that were released from decomposing litter, although additional experiments with nutrient additions to tree seedlings would be needed to further substantiate this conclusion.

4.2. Modes of dispersal of the tree species regenerating under each treatment

The results of this work confirmed the fifth hypothesis of this research, that the majority of the species regenerating under the plantations were animal-dispersed. This coincides with results of similar investigations in other tropical and subtropical humid regions (Denslow and Moermond, 1985; Loiselle and Blake, 1993; Keenan et al., 1999). For example, in the present work, Melastomataceae was the most abundant family in the understory of the mixed plantation and the pure plantation of *V. ferruginea*, while Rubiaceae was the most abundant under *H. alchorneoides*. Both Melastomataceae and Rubiaceae are abundant in the understory of La Selva forests (Loiselle and Blake, 1993), and they are important in the diet of frugivorous birds, such as manakins and tanagers (Denslow et al., 1986). The fruits of species of these families are typically dispersed by birds: they are highly visible, with high caloric value, small in size, and they are protected against damage when they are in the digestive tract of the birds (Denslow and Moermond, 1985).

In constrast, Piperaceae was the most abundant family under pure plantations of *G. americana* and *B. elegans*. Piperaceae are seldom visited by frugivorous birds, and are preferred by bats (Loiselle and Blake, 1993). The inflorescence of the *Piper* genus contains numerous small flowers (Fleming, 1983). The fruits can be easily removed from the plants at maturity, and probably bats of the Phyllostomatidae group are their most important dispersers (Fleming, 1983). The successful germination of *Piper* seeds depends on their passage along the digestive tract of bats. Another possible reason for the abundance of individuals of the *Piper* genus is its form of propagation. Field experiences have shown that *Piper* species have several forms of vegetative reproduction, including resprouting of stems and roots. The *Piper* species are early successional species and are found in large gaps (Grieg, 1993). Both *B. elegans* and *G. americana* plots had higher light penetration than the other plantation plots. Higher light availability favored the growth of grasses and ferns, impeding the growth of woody species (Guariguata et al., 1995; Powers et al., 1997; Montagnini et al., 1999).

Very few woody species were found in the control, natural regeneration plots. Factors that may impede the establishment of woody species in the control may be the lack of perches for seed dispersers and invasion by herbaceous vegetation which outcompetes the tree seedlings in their growth (Montagnini et al., 1999).

4.3. Choice of adequate plantation species to facilitate woody regeneration

In this research, the species found in the understory of the tree plantations belonged to the three most common families in the understory of secondary forests of the region, Melastomataceae, Rubiaceae and Piperaceae (Laska, 1997). In addition, species of primary forest of the region, such as *Pentaclethra macroloba, Dendropanax arboreus, Dypterix panamensis, Hernandia* sp., *Laetia procera, Nectandra* sp. and *Cordia alliodora* (Finegan and Sabogal, 1988; González and Chaves, 1994; Hartshorn and Poveda, 1983; Peralta et al., 1987) were found in the understory of the mixed plantation and under the pure plantations of *H. alchorneoides* and *V. ferruginea*. These are promising indicators for the use of these plantations as accelerators of natural forest succession in the region. The greatest abundance of regenerating individuals and species richness was found in the understory of the mixed plantation for the first two height classes of tree individuals considered here. Apparently, the diversity of conditions that were found in the mixed plantation with respect to canopy shading and litter accumulation, would foster the establishment of different species. In the mixed plantation there would be also a greater diversity of perches for seed dispersers.

Tree regeneration was also abundant under the pure plantations of *V. ferruginea* and *H. alchorneoides*. In another study in other plantations at La Selva, Powers et al. (1997) found that the greatest plant diversity in the understory was in pure plantations of *Vochysia* spp. The authors attributed this result to the abundant branching of these species, that tends to increase shading in the understory and favor the establishment of frugivorous birds and bats from early stages of their growth (Powers et al., 1997).

Both *V. ferruginea* and *H. alchorneoides* had the thickest litter layers, a fact that coincides with earlier results of studies of litterfall and litter accumulation in this plantation (Horn and Montagnini, 1999). The majority of the individuals established under *H. alchorneoides* belonged to height class 3 (>2 m) which implies that they were those that had the highest survival. In earlier research on nutrient release from tree litter, maize seedlings had higher survival rates and vigor when grown on soil amended with litter from *H. alchorneoides* or *V. ferruginea* (Horn and Montagnini, 1999). This suggests that there is a positive effect of litter of *V. ferruginea* and *H. alchorneoides* on growth of tree species. Although these species showed significant differences in their leaf nutrient composition (N, Mg and K) both had a slower decomposition rate than those of *G. americana* and *B. elegans* (Horn and Montagnini, 1999; Stanley and Montagnini, 1999). This slower decomposition would allow for a slower release of nutrients over a longer period of time. In a site with 4000 mm annual rainfall it is expected that a considerable proportion of the nutrients released from litter are washed away or leached out if they are not absorbed by plants. The abundant litterfall with relatively slow decomposition of *H. alchorneoides* and *V. ferruginea* may allow for greater incorporation of nutrients to the regenerating individuals growing in their understories over a longer period of time (Horn and Montagnini, 1999; Stanley and Montagnini, 1999).

Other factors to be taken into account when evaluating the role of plantations in facilitating natural regeneration include the future management of the plantation trees as well as the regenerating seedlings and saplings. The costs and benefits of managing the regenerating seedlings and saplings as an alternative to clearing and replanting should be assessed. In addition to considering the ecological factors influencing tree regeneration, the socioeconomic feasibility of these plantations as practical systems for the recovery of biodiversity in deforested landscapes in the region should be also examined.

5. Conclusions

In this research, tree plantations facilitated forest regeneration, influencing numbers of tree individuals as well as species diversity. Regeneration of native tree species was more abundant under the tree plantations than in the natural regeneration control. There was a larger abundance of individuals and species diversity in the mixed than in the pure plantations. Although in the mixed plantation there was a higher recruitment of tree individuals in the two smaller height classes: class 1: 15 cm–1 m, class 2: 1.05 cm–2 m, there was a greater density of taller individuals (height class 3, >2 m) under the plantation of *H. alchorneoides*. Apparently a greater shading index found under this species (three and four, in the scale used here) favored germination and growth of regenerating individuals, and the relatively deep litter layer (7 cm) would also provide favorable conditions for seedling survival. The majority of the regenerating individuals were dispersed by birds and bats. The different tree plantations generated different shading and litter accumulation conditions, influencing germination and survival of regenerating individuals. Very few woody species were found in the control, natural regeneration plots. Factors that may impede the establishment of woody species in the control may be the lack of perches for seed dispersers and invasion by herbaceous vegetation which outcompetes the tree seedlings in their growth.

Acknowledgements

The authors thank Orlando Vargas and Joel Alvarado of La Selva Biological Station for their help in species identification, Luis Angel Arias Madrigal for his help in the field work and Ignacio M. Barberis, José Vesprini, Frank Berninger and Celia Harvey for their comments on the manuscript. This research was supported by F.O.M.E.C. (Argentina) and CATIE (Costa Rica).

References

Bertsch, F.H., 1986. Manual para interpretar la fertilidad de los suelos en Costa Rica. Universidad de Costa Rica. Escuela de Fitotecnia, San José, Costa Rica 76 pp.

Chávez, A.G., 1998. Efecto de plantaciones forestales sobre la calidad de la regeneración leñosa en la Estación Biológica La Selva, Costa Rica. Tesis MSc., Centro Agronómico Tropical de Investigación y Enseñanza, Escuela de Posgrado, Turrialba, Costa Rica, 60 pp.

Denslow, J.S., Moermond, T.C., 1985. Fruit display and foraging strategies of small frugivorous birds. In: Arayand, W.G. D., Correa, M.D. (Eds.), The Botany and Natural History of Panama, Missouri Botanical Garden, St. Louis, pp. 245–253.

Denslow, J.S., Moermond, T.C., Levey, D.J., 1986. Spatial components of fruit display in understory trees and shrubs. In: Estrada, A., Fleming, T.H. (Eds.), Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrechtpp, pp. 37–44.

Finegan, B., Sabogal, C., 1988. El desarrollo de sistemas de producción sostenible en bosques tropicales húmedos de bajura: un estudio de caso en Costa Rica. El Chasqui (Costa Rica) 17, pp. 3–24

Fleming, T.H.,1983. Piper. In: Janzen, D.H. (Ed.), Costa Rican Natural History. University of Chicago Press, Chicago, pp. 303–305.

Grieg, N., 1993. Regeneration mode in neotropical Piper: habitat and species comparisons. Ecology 74, 2125–2135.

González, E., Chaves, E., 1994. Estructura y composición de un bosque húmedo tropical explotado en la región norte de Costa Rica. Yvyraretá (Argentina) 5, 57–69.

González, E., Fisher, R.F., 1994. Growth of native forest species planted on abandoned pastureland in Costa Rica. For. Ecol. Manage. 70, 150–167.

González, E., Butterfield, R., Segleau, J., Espinoza, M., (Eds.) 1990. Primer Encuentro Regional sobre Especies Forestales nativas de la Zona Norte y Atlántica. Memoria, 28–29 julio 1990, Chilamate, Costa Rica. Inst. Tecnol. Costa Rica, Cartago, Costa Rica.

Guariguata, M., Rheingans, R., Montagnini, F., 1995. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. Restor. Ecol. 3, 252–260.

Hartshorn, G.S., Poveda, L.J., 1983. Checklist of trees. In: Janzen, D.H. (Ed.), Costa Rican Natural History. University of Chicago, Chicago, pp. 158–183.

Harvey, C.A., Haber, W.A., 1999. Remnant trees and the conservation of biodiversity in Costa Rican pastures. Agrofor. Sys. 44, 37–68.

Holl, D., 1998. Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture ? Restor. Ecol. 6, 253–261.

Holl, K., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31, 229–242.

Horn, N., Montagnini, F., 1999. Litterfall, litter decomposition and maize bioassay of mulches from four indigenous tree species in mixed and monospecific plantations in Costa Rica. Int.Tree Crops J. 10, 37–50.

Jussi, K., Goran, A., Yasuf, J., Antti, O., Kari, T., Risto, V., 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: understorey development in forest plantations. J. Veg. Sci. 6, 205–210.

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

Laska, M.S., 1997. Structure of understory shrub assemblages in adjacent secondary and old growth tropical wet forests, Costa Rica. Biotropica 29, 29–37.

Loiselle, B.A., Blake, J.G., 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a neotropical lowland wet forest. Vegetatio 107/108, 177–189.

Lugo, A.E.,1992. Tree plantations for rehabilitating damaged forest lands in the tropics. In: Wali, M.K. (Ed.). Ecosystem Rehabilitation. SPB Academic Publishing, The Hague, The Netherlands.

Mc Clanahan, T.R., Wolfe, R.W., 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conservation Biol. 7, 279–285.

Montagnini, F., Sancho, F., 1990. Influencia de seis especies de árboles nativos sobre la fertilidad del suelo en una plantación experimental en la llanura del Atlántico en Costa Rica. Yvyraretá (Argentina) 1, 29–49.

Montagnini, F., 1994. Agricultural systems in the La Selva region. In: McDade, L.A., Bawa, K., Hespenheide, H.A., Hartshorn, G.S. (Eds.). La Selva: ecology and natural history of a neotropical rainforest. University of Chicago Press, Chicago, pp. 307–316.

Montagnini, F., González, E., Porras, C., Rheingans, R., 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. Commonwealth For. Rev. 74, 306–314.

Montagnini, F., Guariguata, M., Ribeiro, N., Mariscal, A., 1999. Regeneración natural en plantaciones puras y mixtas de especies nativas. Actas IV Semana Científica, Programa de Investigación, Centro Agronómico Tropical de Investigación y Enseñanza (CATIE). Turrialba, Costa Rica, pp. 324–327.

Nepstad, D., Uhl, C., Serrao, E., 1991. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Pará, Brasil. In: Anderson, A.B. (Ed.) Alternatives to deforestation: Steps Toward Sustainable use of the Amazon Rain Forest. Columbia University Press, New York, pp. 215–229.

Otsamo, R., 2000. Secondary forest regeneration under fast-growing forest plantations on degraded *Imperata cylindrica* grasslands. New Forests 19, 69–93.

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

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

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

Parrotta, J.A., 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. For. Ecol. Manage. 124, 45–77.

Peralta, R., Hartshorn, G.S., Lieberman, D., Lieberman, M., 1987. Reseña de estudios a largo plazo sobre composición florística y dinámica del bosque tropical de La Selva, Costa Rica. In: Clark, D.A., Dirzo, R., Fetcher, N. (Eds.). Ecología y Ecofisiología de Plantas en los Bosques Mesoamericanos. Rev. Biol. Trop. 35 (Suppl. 1), pp. 23–40.

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 plantation in Costa Rica. For. Ecol. Manage. 99, 43–54.

Ribeiro, N., 1998. Evaluación de la regeneración natural de especies arbóreas de plantaciones puras y mixtas en áreas de recuperación en La Selva, Costa Rica. Informe de Tópico Especial, IV Trimestre, Programa de MSc., Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba, Costa Rica, 15 pp.

Sancho, F., Mata, R., 1987. Estudio detallado de suelos. Estación Biológica La Selva. Organización para Estudios Tropicales, San José, Costa Rica, 162 pp.

Scheffe, H.,1959. The analysis of variance. Wiley, New York.

Shannon, E., 1948. A mathematical theory of communications, Bell System Technol. J. 27, pp. 379–423 and 623–653.

Stanley, W.G., Montagnini, F., 1999. Biomass and nutrient accumulation in pure and mixed plantations of indigenous tree species grown on poor soils in the humid tropics of Costa Rica. For. Ecol. Manage. 113, 91–103.