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Forest Ecology and Management 191 (2004) 171–183
Forest Ecology and Management
www.elsevier.com/locate/foreco

Facilitating natural regeneration in *Saccharum spontaneum* (L.) grasslands within the Panama Canal Watershed: effects of tree species and tree structure on vegetation recruitment patterns

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Received 16 June 2003; received in revised form 28 August 2003; accepted 2 December 2003

Abstract

To counteract the escalating rates of tropical deforestation, it is essential that we not only minimize forest loss, but that we create effective reforestation strategies. This study investigates understory recruitment patterns in mixed native species plantations along the Panama Canal that were established in grasslands dominated by the invasive exotic species *Saccharum spontaneum* (L.) Graminae. We test the hypothesis that regeneration rates vary significantly by overstory tree species and overstory tree structure, and explore the mechanisms generating such patterns. Of the seven tree species sampled, *Inga* spp. recruits significantly more tree seedlings than any other species. Additionally, crown foliage density appears to be the most significant structural factor determining rates of understory tree species regeneration. A survey of bird activity in the plantations and in unplanted areas indicates that birds generally visit large trees and that those tree species most frequently visited by birds also have the greatest density of understory tree seedlings. These results support the hypothesis that tree structure significantly affects regeneration patterns, and suggests that bird dispersal may be a fundamental driver in seedling recruitment. Furthermore, results indicate that the presence of any tree species in a reforestation plot increases the understory species richness and species cover relative to non-reforested areas, while significantly reducing the degree of *S. spontaneum* dominance. While active reforestation appears to facilitate forest regeneration in areas occupied in *S. spontaneum*, tree species and tree structure are important factors to consider when designing reforestation programs that are intended to facilitate natural regeneration.

Keywords: *Saccharum spontaneum*; *Inga punctata*; *M. calabura*; *A. excelsum*; *Cordia* spp.; *D. panamensis*; *H. crepitans*; *L. seemannii*; Understory development; Natural regeneration; Reforestation; Tropical plantations; Panama; Panama Canal Watershed

1. Introduction

Minimizing deforestation effects is a major challenge for tropical regions worldwide. The Republic of Panama has lost more than 30% of its forested area to

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0378-1127/$ – see front matter
doi:10.1016/j.foreco.2003.12.002

land and agro-pastoral development in the past 50 years (Romero et al., 1999; Condit et al., 2001). Reforestation efforts are critical to improving species diversity, soil productivity and water quality, particularly in the Panama Canal Watershed, where deforestation and development have been associated with increasing rates of erosion and sediment delivery to streams (Montagnini and Sancho, 1990; Stallard et al., 1999). Successful forest regeneration depends upon multiple site and species attributes, including characteristics of planted trees and their proximity to seed sources (Guariguata et al., 1995; Zimmerman et al., 2000), yet little information exists regarding effective native species management (Keenan et al., 1997; Hooper et al., 2002). This study explores the factors that promote understory recruitment in a native species plantation within the Panama Canal Watershed in an effort to identify successful strategies that best promote the development of dense and diverse understory vegetation.

Our primary objective was to identify plantation tree species and structural characteristics associated with high understory vegetation density and diversity, particularly of woody species. Studies indicate that tree plantations facilitate seedling recruitment and that various overstory attributes, including shade, structural complexity, leguminous trees, understory vegetation, and tree species, play an important role in determining regeneration rates (Ashton et al., 1997; Asquith et al., 1997; Carnevale and Montagnini, 2002; Denslow, 1986; Guariguata et al., 1995; Haggar et al., 1997; Hooper et al., 2002; Kuusipalo et al., 1995; Lamb, 1998; Otsamo et al., 1997; Parrotta, 1992, 1993, 1995, 1999; Parrotta et al., 1997; Wheelwright et al., 1984; Wunderle, 1997). Because the significance of each of these components is unknown, it is important to determine those attributes of overstory tree species and structure that best promote understory recruitment.

Our second objective was to conduct an initial assessment of the relative attractiveness of particular plantation tree species and tree structural characteristics to birds. Not only is seed dispersal a critical component to tree establishment, but dispersal by birds has been found to account for 80–90% of tree species in tropical plantations (Carnevale and Montagnini, 2002; Guariguata et al., 1995; Howe, 1997; Keenan et al., 1997; McClanahan and Wolfe, 1993; McDonnell and Stiles, 1983; McDonnell, 1986; Parrotta, 1993; Parrotta et al., 1997; Wunderle, 1997; Zimmerman et al., 2000). It is therefore important to plant tree species that attract birds as a mechanism for facilitating natural regeneration.

Our third objective was to assess the performance of seven native tree species in terms of their ability to establish in *Saccharum spontaneum* grasslands and reduce *S. spontaneum* dominance. Efforts to restore forest cover within the PCW are greatly complicated by the presence of *S. spontaneum* (L.) Graminae, an exotic and invasive Asian wild sugarcane that has invaded deforested areas, particularly former construction sites along the Panama Canal. Previous research demonstrates that grasses significantly inhibit establishment and growth of tree seedlings in plantations by quickly dominating cleared and subsequently abandoned lands (Aide et al., 1995; Carnevale and Montagnini, 2002; Guariguata et al., 1995; Hooper et al., 2002; Otsamo, 2000; Zimmerman et al., 2000). Little research has been conducted on the ecology of *S. spontaneum* in Panama, though mature *S. spontaneum* may inhibit dispersal by animals and thus prevent large-seeded species from establishing in *S. spontaneum* grasslands (Hammond, 1995; Hooper et al., 2002; Cullman, unpublished data; Palacios, unpublished data).

2. Methods

2.1. Site description

Data was collected at Red Tank, a former US Military sanitary landfill, where dry trash, such as cardboard, yard waste, car parts, timber, and military surplus, was deposited between 1953 and 1995 (Phillips, 2001). The site is located in the moist tropical forest life zone (Holdridge, 1967), at approximately 9°1′N, 79°36′W and 100 m a.s.l. The average temperature is 27 °C with a 9 °C average diurnal variation. Average precipitation is 2600 mm per year, with 90% of this precipitation occurring between May and December (Dietrich et al., 1996). At the close of operations in 1995, the landfill was capped with clayey soils excavated from nearby hillsides and spread to a depth of 36 in. (Phillips, 2001). The resulting soils are highly compacted and are nearly flat along the tops of fill areas, and have slopes ranging from 16° to 22°

along the sides of fill areas. Soil parent materials of the area include both sedimentary and igneous rocks, primarily limestone, claystone, sandstone, shale, basalt, andesite and granodiorite (USDA, 1974). These materials weather to form red clay, which contains little sand but pulverizes easily. Long-term leaching has removed much silica and lime, leaving iron and aluminum (USDA, 1974). Soil surveys indicate that the site contains high macronutrient levels, including K, P, Ca and Mg, high acidity and low soil organic matter (Phillips, 2001). Aerial photos indicate that by 1997 *S. spontaneum* dominated the site.

2.2. Plantation establishment

In May 1998, the Canal Authority established 13 ha of mixed plantations dispersed in eight blocks throughout the landfill. Fourteen tree species were used: *Anacardium excelsum* (Bertero and Balb.) ex Kunth, *Ochroma pyramidale* (Cav. ex Lam.) Urb., *Cordia* spp., *Miconia argenta* DC., *Hura crepitans* L., *Spondias mombin* L., *Inga* spp., *Guazuma ulmifolia* Lam., *Enterolobium cyclocarpum* (Jacq.) Griseb., *Luehea seemannii* Triana and Planch, *Vatairea* spp., *Dipteryx panamensis* (Pittier), *Apeiba tibourbou* Aubl., and *Muntingia calabura* L. Species were selected based on their expected attractiveness to seed dispersers and for their rapid growth rates.

Prior to planting, *S. spontaneum* was manually cleared and seedlings were planted at a 3 m spacing with 1–2 kg of organic fertilizer. Species alternate in parallel rows with a regular pattern following the order of species as listed above. Plantation maintenance has involved the periodic cutting of *S. spontaneum* and other grasses 12 times in the first 18 months and once every 3–6 months thereafter.

2.3. Tree species selection

Seven of the fourteen utilized species were selected based upon initial observation of the plantations to reflect a range of structural characteristics and growth habits (Table 1). Three of the selected species had produced fruit by the time of the census. *H. crepitans*, which produces 'explosive' capsules that mechanically disperse seed, began producing fruit in the second year after planting. *M. calabura*, which produces abundant, sweet red berries consumed by many birds and some mammals, began producing fruit in its first year. The *Inga* spp. (primarily *Inga punctata*) began producing long pods (7–18 cm) in its first year, each containing multiple seeds covered in a soft, pulpy aril that are consumed by some mammals. *M. calabura* and *Inga* spp. were selected in part to examine whether fruit production is related to understory development. As Table 1 indicates, most tree characteristics are strongly correlated. *M. calabura* and *Inga* spp., the two species that have produced fruit known to be consumed by animals, have also grown the fastest.

2.4. Vegetation sampling

Five of the eight plantation blocks were selected for the study based upon size (minimum dimensions of 150 m × 40 m was required to avoid excessive edge effects), sufficient numbers of each tree species and

Table 1
Characteristics of tree species selected for study

Species	Height (m)	Crown diameter (m)	Crown density	Dispersal syndrome
A. excelsum	3.0 bc	1.8 c	Open	Mammals, water
Cordia spp.	1.8 e	1.3 cd	Open	Wind
D. panamensis	2.6 cd	1.0 d	Open	Mammals
H. crepitans	2.1 de	1.6 cd	Moderate	Mechanical
Inga spp.	3.6 a	4.4 a	Dense	Mammals
L. seemannii	2.8 bc	1.5 cd	Open	Wind
M. calabura	3.3 ab	3.8 b	Moderate	Birds, mammals

Mean height and crown diameter are presented in meters. Means with the same letter are not significantly different at a 95% confidence interval. Crown density was ocularly estimated and classified as open (<1/3 of the crown volume occupied by branches and foliage), moderate (between 1/3 and 2/3 of the crown volume occupied by branches and foliage) or dense (>2/3 of the crown volume occupied by branches and foliage). Seed dispersal syndromes are provided for those species that had produced fruit by the time of data collection.

accessibility. A 15 m buffer was excluded from around the edge of each of the five blocks, and the remaining interior spaces were divided into 30 sample areas of equal size. Plantation blocks varied in size; therefore the number of sample areas per plantation block ranged from 4 to 6 to maintain equal sampling intensity across all plantation blocks. A single transect was randomly located within each sample area and established perpendicular to the orientation of alternating pure species rows. A single individual of each of the seven tree species was sampled along each transect, for a total of 30 individuals of each species and 210 trees total.

Total height, height to live crown (to the first branch with live foliage) and crown diameter in two directions were measured for each sampled individual. Crown density was ocularly estimated by assigning each individual to one of four crown density classes according to the area of a cylinder encompassing each crown estimated to be occupied by foliage and branches (1 refers to leaf cover from 0 to 25%, 2 from 25 to 50%, 3 from 50 to 75% and 4 from 75 to 100%). A crown density index was calculated by multiplying this density scalar by the volume of the cylinder encompassing the crown $[(\text{total height} - \text{height to crown}) \times (\text{average crown width})]$.

The understory at each tree was sampled using eight $0.5\,\text{m} \times 0.2\,\text{m}$ ($0.1\,\text{m}^2$) frames made of PVC tubing. Frames were located 0.75 and 1.5 m from the center of the tree trunk in each of the four cardinal directions. Within each frame, the percentage of the surface area occupied by each species was estimated, and all species were identified in the field or collected for later identification at the herbariums of the Smithsonian Tropical Research Institute and the University of Panama, both located in Panama City, Panama. Because *S. spontaneum* and other grasses were regularly cut, the percentage of area occupied by the corms of each species was used as the measure of percent cover. The percent cover of litter, soil, rocks and woody debris was also estimated such that the final total percent cover, all components included, was 100%. Total number of species and total percent cover of species were then tallied and recorded for each frame.

Five areas in which the *S. spontaneum* had not been cleared and plantations had not been established were selected for comparison. Areas were selected using the same criteria used in selecting plantation blocks, and a 15 m buffer was excluded from around the edge of each area. In each *S. spontaneum* dominate area, a transect 30 m long and 1 m wide was randomly located and sample points were established every 6 m to match the spacing between the sampled trees. Eight $0.1\,\text{m}^2$ plots were placed in an arrangement equivalent to that in the plantation at each sample point, and vegetation, woody debris, soil, rocks and litter were sampled in the same fashion.

2.5. Initial assessment of bird activity

A comprehensive study of seed dispersal within the plantations was beyond the scope of the present study; therefore an initial assessment of bird activity was conducted to yield insight into the behavior of this important group of seed dispersers within the plantation and in areas still dominated by *S. spontaneum*. Bird activity was observed in each of the five plantation blocks and five *S. spontaneum*-dominated areas from 6:30 to 7:30 a.m. between June and August 2001. Four observation positions were selected within or directly adjacent to each area to allow for maximum visibility of the trees in the plot. Bird activity was observed for 15 min from each position, with the order in which each point was visited rotating each day for 4 days. On the fifth morning in each area, a transect was walked throughout the entire area for 60 continuous minutes. Total observation time in each area equaled 300 min over five mornings.

Birds were observed by recording their visitation to trees, *S. spontaneum* or other grasses within the area under observation. When a bird perched on any tree, the species of the tree was recorded, and the height, crown width and crown density of each visited tree was ocularly estimated on a scale of 1–4. The estimates for each category correspond to the following:

- height—1: 0–1 m, 2: 1–2 m, 3: 2–3 m, 4: >3 m;
- crown width—1: 0–0.5 m, 2: 0.5–1 m, 3: 1–1.5 m, 4: >1.5 m;
- crown density—1: 0–25% leaf cover, 2: 25–50% leaf cover, 3: 50–75% leaf cover, 4: 75–100% leaf cover. Dead trees were assigned a value of 0.

A new record was made each time a bird visited a tree. Because the *S. spontaneum* in a given area tended to be of the same height, a single estimate was made of the height of the *S. spontaneum* in that area.

The height, crown width and crown density were ocularly estimated for 100 of each of the 14 tree species planted in Red Tank (20 individuals in each of the five areas) using the same indices as used during bird observations, to allow for comparison of the composition of the plantation characteristics as a whole with characteristics of the trees selected by birds.

2.6. Data analysis

Mean values were calculated by species for each measured tree characteristic (height, height to live crown, crown width, crown density) and examined for significant differences using Duncan Pairwise comparisons ($\alpha = 0.05$; SAS Institute, 2001). Understory vegetation data was classified into groups according to habit (grasses, legumes, herbaceous plants and woody plants) and woody species were further classified by dispersal syndrome (wind, bird or mammal). For each overstory tree, the following was calculated: percent cover for each vegetation type, total species cover, total species number and litter cover. Duncan pairwise comparisons were used to test for differences in understory composition according to overstory species and stepwise multiple regression was used to assess differences in understory composition according to overstory tree characteristics.

Seedling recruitment data was analyzed by assessing the relationship between (1) overstory species, (2) tree height, (3) tree crown width, (4) tree crown density, (5) litter cover and (6) grass cover (independent variables) on (a) understory tree cover (trees being any woody species), (b) legume cover, (c) herb cover, (d) grass cover, (e) species richness and (f) total species cover (dependent variables). A one-way ANOVA (SAS Institute, 2001) was used to examine species effects. Linear regressions were conducted to examine litter and grass cover effects, and a multiple regression analysis was used to examine the relative effects of tree height, tree crown width and tree crown density on vegetation recruitment patterns.

Bird activity data from the five areas were synthesized and the number of bird visits calculated for each tree species, height, crown width and crown density category. These visitation rates were compared to tree presence to assess the relative significance of bird's tree preferences. These results were then compared to recruitment patterns to provide insight on ecological dynamics within the reforested plots.

3. Results

3.1. Tree characteristics

Inga spp. was the tallest tree, with an average height of 3.6 m, and was significantly greater than all other species except *M. calabura* (3.3 m, $P < 0.0001$) (Table 1). *Cordia* spp. and *H. crepitans* were the two smallest species (mean heights of 2.2 and 1.7 m, respectively). *Inga* spp. had significantly broader crown than all other species, with an average crown width of 4.4 m ($P < 0.0001$) (Table 1). *M. calabura* was the second widest tree, with an average width of 3.8 m. The crown widths of all other tree species were not significantly different from one another. *Inga* spp. had the greatest crown density index of 57.5, which was twice as great as that of *M. calabura*, the species with the next highest crown density index of 28.1 ($P < 0.0001$) (Table 1). No other tree species was significantly different from any other with regard to crown density index.

3.2. Understory regeneration

Understory tree cover was significantly greater under *Inga* spp. than under any other tree species, with an average cover of 6.3% of the total area sampled ($P < 0.0001$) (Fig. 1). No other tree species were significantly different from each other with regard to understory tree cover. *Inga* spp. also had significantly less total understory vegetation cover than any other tree species, with an average cover of 28.4% ($P < 0.0001$) (Fig. 1); other tree species did not differ significantly from one another.

The multivariate regression analysis shows that understory tree cover increases significantly with tree height, crown density and crown width ($R^2 = 0.274$, $P < 0.0001$) (Table 2). It also shows that crown density best predicts tree recruitment, followed by tree height and crown width, respectively (Table 2). Among woody species, bird-dispersed species were most abundant under all trees, followed by wind-dispersed trees and finally mammal-dispersed trees, respectively (Fig. 2). The three most common understory woody

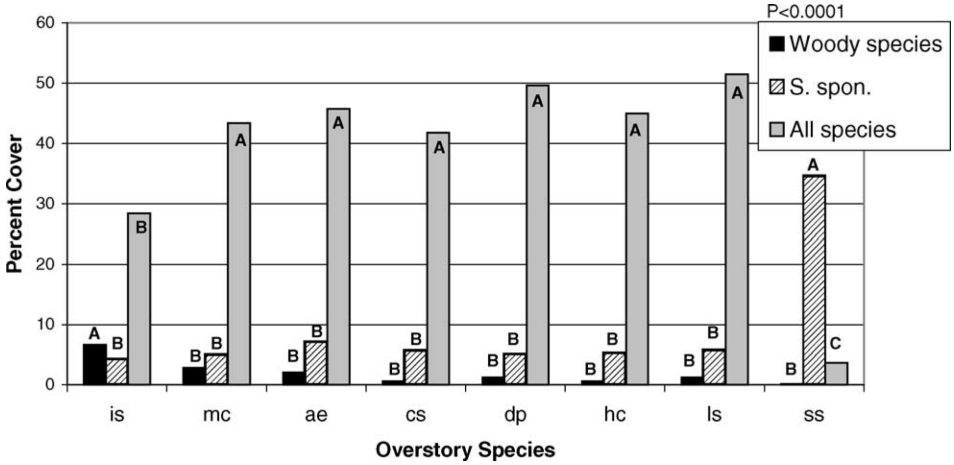

Fig. 1. Mean percent cover of understory woody species, *S. spontaneum*, and total understory species (excluding *S. spontaneum*) grouped by overstory species. Means with the same letter are not significantly different at a 95% confidence interval ($P < 0.001$). Species codes: *A. excelsum* (ae); *Cordia* spp. (cs); *D. panamensis* (dp); *H. crepitans* (hc); *Inga* spp. (is); *L. seemannii* (ls); *M. calabura* (mc); *S. spontaneum* (ss).

Table 2
Regression analysis in SAS, GLM procedure

Dependant variable: understory tree cover	Source (type III SS)	F	Pr > F
$R^2 = 0.2740$	Crown width	0.22	0.6359
$F = 29.69$	Height	3.46	0.0640
$P < 0.0001$	Crown density	20.86	<0.0001

species were *Schefflera morototoni*, *Bursera simaruba* and *Cedrela odorata* (Table 3); these trees are early-successional species and are typically abundant in secondary forests.

Grasses (Graminae) were the dominant understory vegetation type, comprising 28% of all species occurrences. The three dominant legume species (*Desmodium axilare*, *Alysicarpus vaginalis* and *Mimosa*

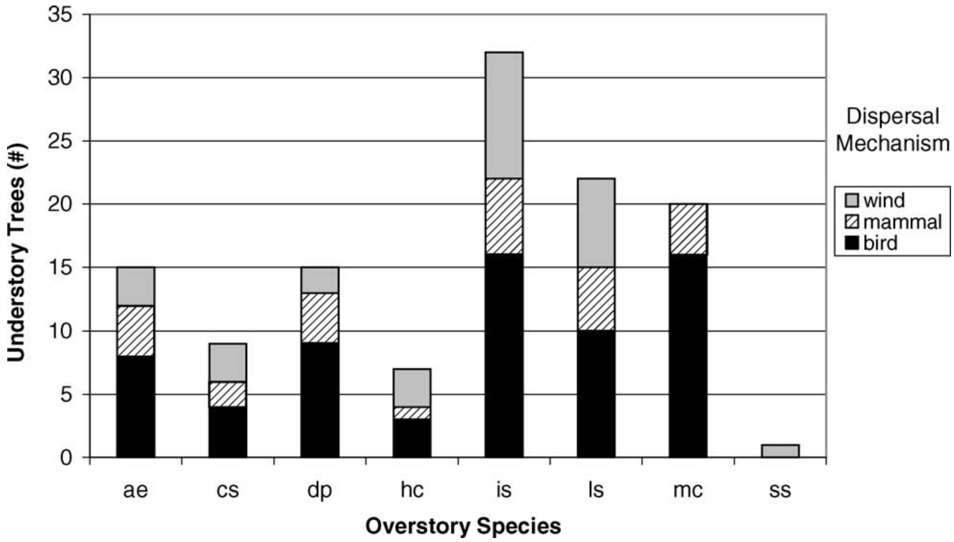

Fig. 2. Total number of woody individuals encountered below each planted tree species, grouped by dispersal mechanism. Species codes: *A. excelsum* (ae); *Cordia* spp. (cs); *D. panamensis* (dp); *H. crepitans* (hc); *Inga* spp. (is); *L. seemannii* (ls); *M. calabura* (mc); *S. spontaneum* (ss).

Table 3
Frequency of species (or family) occurrence in the maximum of 1920 sample frames

Species or family	Vegetation type	Frequency of occurrence
Graminae	Grass	1348
S. spontaneum	Grass	727
D. axilare	Legume	663
A. vaginalis	Legume	514
M. pudica	Legume	427
Verbanaceae	Herb	409
Acanthaceae	Herb	373
Spiracantha cornifolia	Herb	304
Conyza apurensis	Herb	264
Aeschinomene americana	Legume	194
Chamaesyce hitra	Herb	185
Desmodium spp.	Legume	97
Phyllanthus niruri	Legume	87
Stylosanthes guyanensis	Legume	61
Cyperaceae	Grass	58
Sporobolus indicus	Grass	49
Melochia nodiflora	Herb	43
Phyllanthus spp.	Legume	39
Spermacoce prostrata	Herb	31
S. morototoni	Tree	30
Miconia spp.	Herb	26
Paullinia costaricensis	Herb	26
Hyptis recurvata	Herb	23
Phyllanthus urinaria	Legume	19
B. simaruba	Tree	16
C. odorata	Tree	14
Ipomea spp.	Herb	12
Ligodium venustum	Herb	10
Melastomataceae	Herb	10
Pitirograma spp.	Herb	9
Combetum spp.	Tree	8
Heliconia spp.	Herb	8
Cochlospermum vitifolium	Tree	7
Lycopodium cernum	Herb	7
M. argenta	Tree	7
G. ulmifolia	Tree	6
Cissus erosa	Herb	5
Doliocarpus spp.	Tree	5
S. mombin	Tree	5
Amaioua corymbosa	Tree	4
Aypana amigdalina	Herb	4
Helicteres guazumaefolia	Herb	4
Paullinia spp.	Herb	4
Terminalia amazonia	Tree	4
Cordia bicolor	Tree	3
Cuaretela spp.	Tree	3
A. tibourbou	Tree	2
Compuista spp.	Herb	2
Hura crepitans	Tree	2
M. calabura	Tree	2
Sida spp.	Herb	2
Terracera volubilis	Herb	2
Trema micrantha	Tree	2
Allophyllus occidentalis	Tree	1
Antirhea trichantha	Tree	1
Arrabidaea candicans	Tree	1
Corchorus orinocensis	Herb	1
Cupanio spp.	Tree	1
Davilla spp.	Herb	1
E. cyclocarpum	Tree	1
Helicarpus americanus	Tree	1
Inga spp.	Tree	1
L. seemannii	Tree	1
Miconia minutifolia	Tree	1
Unknown species (94)	–	1333

pudica) had a total 21% frequency of occurrence. Herbaceous families Verbanaceae and Acanthaceae consisted of 10% of total understory species (Table 3). Understory species richness, percent grass cover and legume cover did not vary significantly with overstory tree species. Understory species richness, percent species cover, grass cover, herb cover and legume cover did not vary significantly with overstory tree characteristics (Table 4). Litter cover and grass cover were insignificant predictors for all dependent variables.

3.2.1. *S. spontaneum*

Species richness was significantly less in *S. spontaneum* than under all tree species ($P < 0.0001$)

Table 4
Significance of variables in model (Type III SS) SAS, GLM procedure

Dependent variables	Independent variables		
	Tree height	Tree crown width	Tree crown density
Tree cover	$P < 0.0640$	$P < 0.6359$	$P < 0.0001$
Herb cover	$P < 0.7773$	$P < 0.1138$	$P < 0.0929$
Legume cover	$P < 0.3860$	$P < 0.2373$	$P < 0.4876$
Grass cover	$P < 0.6901$	$P < 0.1269$	$P < 0.9820$
Total species cover	$P < 0.8925$	$P < 0.1954$	$P < 0.8326$
Species richness	$P < 0.1507$	$P < 0.0013$	$P < 0.0001$
Correlation			
Tree height	1.000	0.7951	0.6782
Tree crown width	0.7951	1.000	0.8275
Tree crown density	0.6782	0.8275	1.000

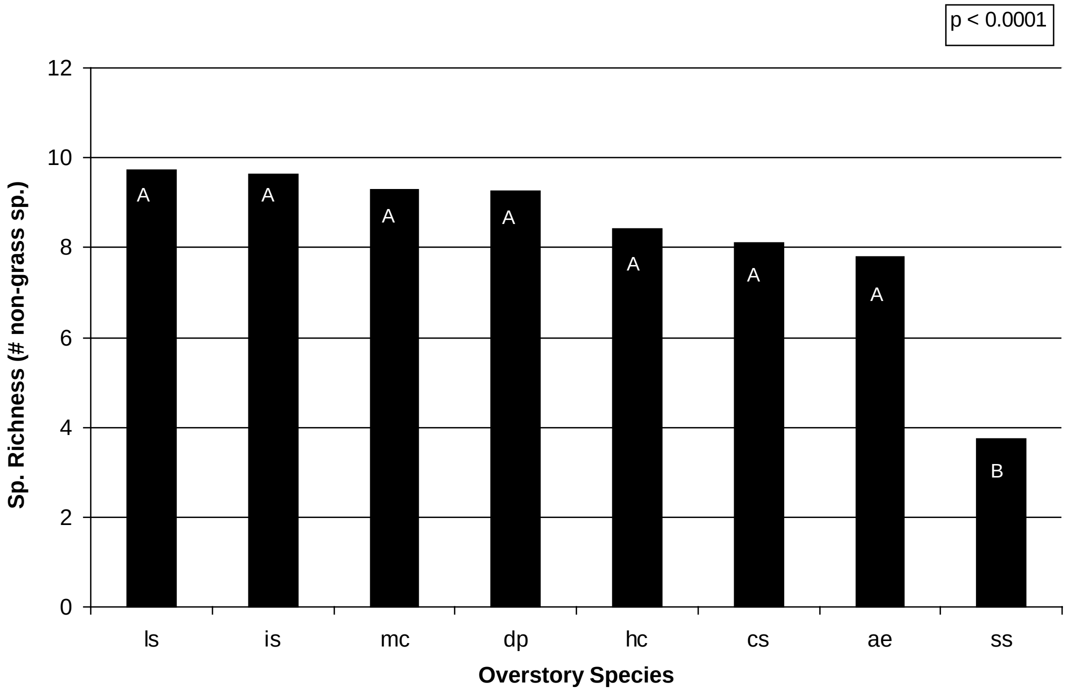

Fig. 3. Mean understory species richness (total number of non-grass species) grouped by overstory species. Means with the same letter are not significantly different at a 95% confidence interval ($P < 0.001$). Species codes: *A. excelsum* (ae); *Cordia* spp. (cs); *D. panamensis* (dp); *H. crepitans* (hc); *Inga* spp. (is); *L. seemannii* (ls); *M. calabura* (mc); *S. spontaneum* (ss).

(Fig. 3). Average species richness in *S. spontaneum* is 3.73 species, whereas species richness under trees ranged from 7.80 to 9.733 species. Vegetation cover for all species excluding *S. spontaneum* was also significantly less in *S. spontaneum* than under all planted tree species ($P < 0.0001$). The average percent cover of all other vegetation in *S. spontaneum* was 5.13%, whereas species cover of all other vegetation in the plantation ranged from 11.5 to 13.1% (Fig. 1). The percent cover of *S. spontaneum* regrowth was significantly less under all tree species than in areas where no trees were planted. The average *S. spontaneum* cover in the reforestation plots was 5.4%, ranging from 4.2 to 7.1%, whereas *S. spontaneum* cover in the areas with no trees was 34.5% (Fig. 1). No other variables were significantly different in *S. spontaneum* when compared to all other tree species.

3.3. Bird activity

Birds visited *Inga* spp. and *M. calabura* three times more often than all other tree species, with 331 and 309 visits, respectively (Fig. 4). Overall, trees in the tallest height class were visited more than two times as often than the other tree classes combined (Fig. 5). Bird visitation was also greatest at the largest crown width and crown density classifications (Fig. 5). Height and crown widths were relatively evenly distributed among all categories (Fig. 6). Trees with crown density classification 1 were the best represented (Fig. 6).

A linear regression of the number of bird visits against the abundance of bird-dispersed woody regeneration by overstory tree species showed a significant correlation ($R^2 = 0.81, P < 0.006$) (Fig. 7). Birds commonly found in *Inga* spp. and *M. calabura* include the crimson-backed tanager (*Ramphocelus d. dimidiatus*), the social flycatcher (*Myiozetetes similis columbianus*), the white-tipped dove (*Leptotila v. verreauxi*) and the clay colored thrush (*Turdus grayi casius*). Birds commonly found in *S. spontaneum* and other grasses include the variable seedeater (*Sporophila americana hicksii*), the ruddy-breasted seedeater (*Sporophila minuta centralis*) and the white-tipped dove (*Leptotila v. verreauxi*).

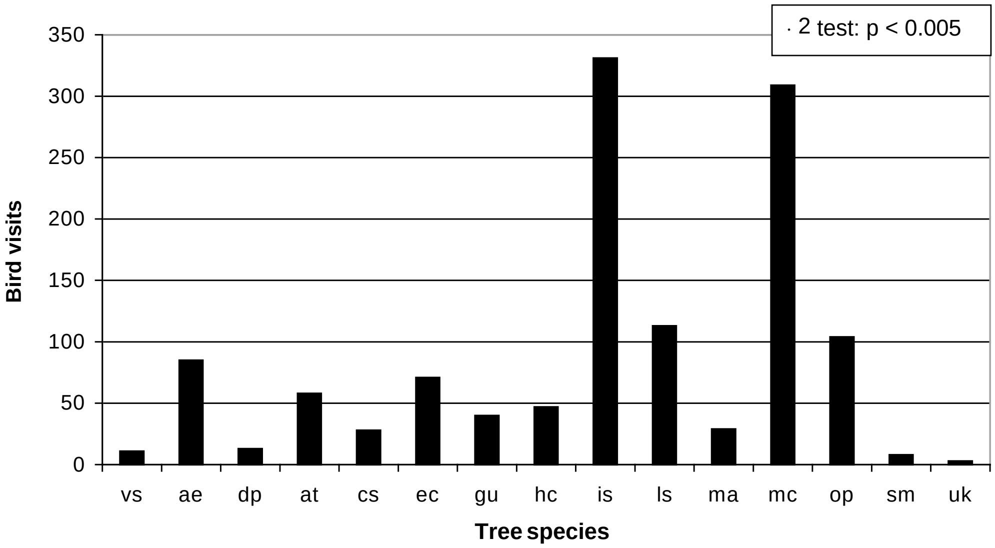

Fig. 4. Total bird visits to each overstory tree species (χ^2-test: $P < 0.005$). Species codes: *A. excelsum* (ae); *Cordia* spp. (cs); *D. panamensis* (dp); *H. crepitans* (hc); *Inga* spp. (is); *L. seemannii* (ls); *M. calabura* (mc); *O. pyramidale* (op); *M. argenta* (ma); *S. mombin* (sm); *G. ulmifolia* (gu); *E. cyclocarpum* (ec); *Vatairea* spp. (vs); *A. tibourbou* (at); unknown (uk).

4. Discussion

In tropical regions, up to 90% of vascular plants rely on animals to disperse their seeds (Estrada and Fleming, 1986). Though equivalent research has not previously been conducted in *S. spontaneum* grasslands, studies in other tropical pasturelands indicate that sites containing perches, structural complexity, edible fruits, understory vegetation, or that are close to primary forest attract more seed dispersers and

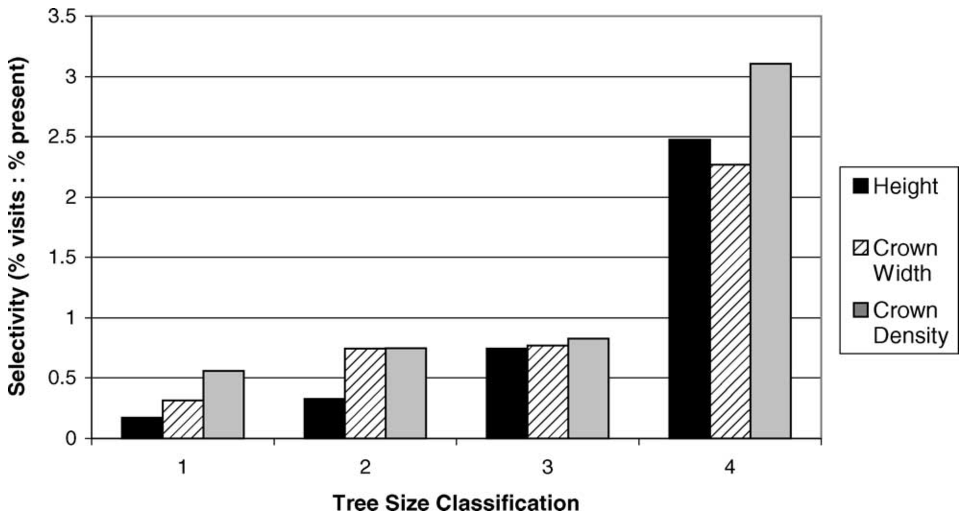

Fig. 5. Total bird visits to tree size classes (see text for class definitions). Selectivity for X size class = (% visits to X)/(% presence of X) (χ^2-test: $P < 0.005$). Tree size classifications—height: 1, 0–1 m; 2, 1–2 m; 3, 2–3 m; 4, >3 m; crown width: 1, 0–0.5 m; 2, 0.5–1 m; 3, 1–1.5 m; 4, >1.5 m; crown density: 1, 0–25% leaf cover; 2, 25–50% leaf cover; 3, 50–75% leaf cover; 4, 75–100% leaf cover. Dead trees were assigned a value of 0.

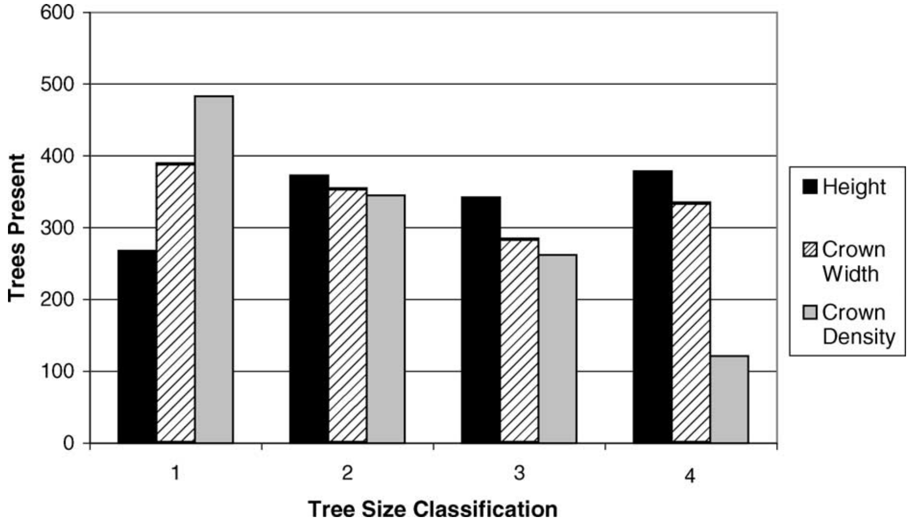

Fig. 6. Trees present in replanted areas, grouped by tree size classifications for height, crown width and crown density. Tree size classifications—height: 1, 0–1 m; 2, 1–2 m; 3, 2–3 m; 4, >3 m; crown width: 1, 0–0.5 m; 2, 0.5–1 m; 3, 1–1.5 m; 4, >1.5 m; crown density: 1, 0–25% leaf cover; 2, 25–50% leaf cover; 3, 50–75% leaf cover; 4, 75–100% leaf cover. Dead trees were assigned a value of 0.

experience more rapid regeneration (Ashton et al., 1997; Carnevale and Montagnini, 2002; Cruz, 1988; Foster and Janson, 1985; Guariguata et al., 1995; Garwood, 1983; Keenan et al., 1997; Kuusipalo et al., 1995; Nepstad et al., 1991; Otsamo, 2000; Parrotta, 1993, 1995; Parrotta et al., 1997; Tucker and Murphy, 1997; Wunderle, 1997; Zimmerman et al., 2000). Results of the present research support the hypothesis that understory regeneration patterns vary by overstory tree structure and potentially by overstory tree species. Of all understory vegetation functional groups, only the density of woody species varied significantly by overstory tree species, with the greatest density occurring beneath *Inga* spp. Additionally, overstory tree height, crown width and crown density vary significantly with woody

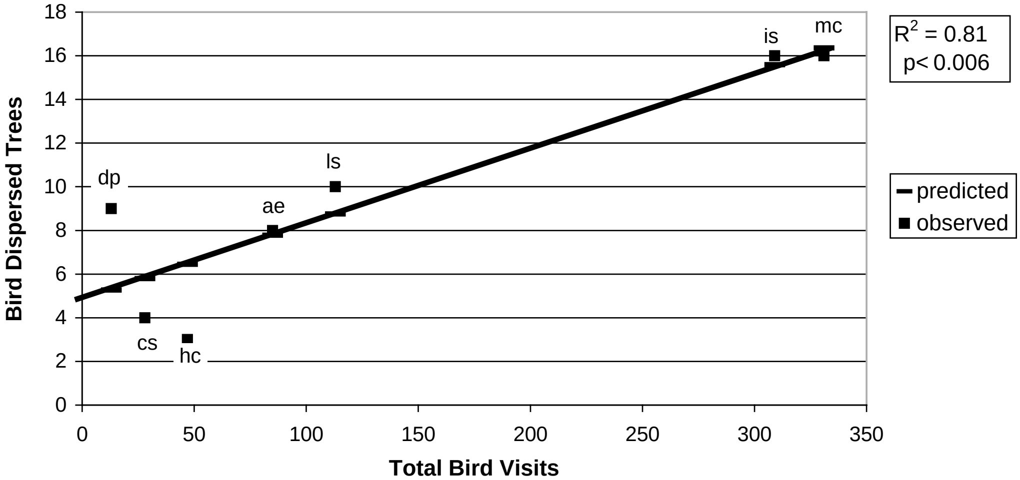

Fig. 7. Linear regression of understory bird-dispersed trees vs. total bird visits ($R^2 = 0.81, P < 0.006$). Species codes: *A. excelsum* (ae); *Cordia* spp. (cs); *D. panamensis* (dp); *H. crepitans* (hc); *Inga* spp. (is); *L. seemannii* (ls); *M. calabura* (mc).

species recruitment rates, with crown density being the best predictor. However, because *Inga*. spp. are significantly different from all other tree species in its high crown density, it is not possible to determine if the high understory tree recruitment can be attributed to characteristics specific to the species or to its structure alone. High rates of woody recruitment observed below *Inga* spp. may be due to the lack of light penetration through its thick canopy, which may shade out pioneer grass species while facilitating growth of shade-tolerant tree species by reducing competition (Aide et al., 1995; Carnevale and Montagnini, 2002; Guariguata et al., 1995; Hooper et al., 2002; Zimmerman et al., 2000), high soil moisture (Ashton et al., 1997), or through some other mechanism (Holl, 1998; Guariguata and Pinard, 1998). *Inga* spp. also fixes nitrogen and may improve soil fertility (Ashton et al., 1997).

The high correlation between bird visitation rates and the density of bird-dispersed understory tree seedlings indicates that bird visits are a strong predictor of bird-dispersed recruitment rates. Furthermore, birds visited trees of greatest height, crown width and crown density, which supports the hypothesis that tree structure strongly influences bird visitation rates and therefore regeneration patterns. Birds visited *Inga* spp. more than all other tree species, which may increase relative seed dispersal rates and further contribute to its high woody species regeneration.

However, tree structure and/or tree species is an important determinant of understory tree recruitment, independent of bird visitation, as indicated by the significantly greater number of trees recruited by *Inga* spp. than by *M. calabura*, despite their similar bird visitation rates. The number of bird-dispersed trees under *Inga* spp. and *M. calabura* were identical, but the additional trees under *Inga* spp. were wind-dispersed species. This suggests that either *Inga* spp. or its high crown density facilitates recruitment of wind-dispersed trees. Additional studies that compare regeneration rates under tree species with structure similar to *Inga* spp. would clarify whether high tree recruitment rates under *Inga* spp. can be attributed to its structure or to species-specific characteristics. Furthermore, species-specific information regarding bird visitation rates would indicate whether the bird species visiting *Inga* spp. and *M. calabura* varied in their life histories, thereby providing insight into the relative effects of other factors affecting germination and regeneration success.

In addition to species and/or structure-dependent recruitment patterns, data indicate that the presence of any tree species in a reforestation plot increases the understory species richness and species cover relative to non-reforested areas, while significantly reducing the rate of *S. spontaneum* invasion. These results therefore emphasize the importance of reforestation in facilitating rainforest regeneration in areas occupied in *S. spontaneum* and suggest that tree species and structure are important factors to consider when choosing trees for reforestation projects.

5. Conclusions

Mixed native species reforestation appears to be an effective means of replacing *S. spontaneum* and facilitating the development of diverse understory vegetation. Understory species richness and density were significantly higher in the plantations than in the unplanted areas, while *S. spontaneum* density was significantly lower in the plantations. However, these results also suggest that patterns of understory vegetation recruitment vary significantly by overstory tree species and tree structure. *Inga* spp. and trees with dense crowns are most likely to facilitate rapid woody species recruitment and *S. spontaneum* exclusion. Bird visits also vary by overstory tree species and tree structure and may play an important role in facilitating woody species recruitment.

Better knowledge regarding the relative impacts of tree structural and species characteristics on regeneration patterns is crucial to guide forest managers when designing reforestation projects. Management recommendations for native species plantations within the PCW include (a) plant *Inga* spp., (b) plant tree species with high crown density and (c) plant tree species that attract birds. Further research is recommended to determine (a) whether species structurally similar to *Inga* spp. facilitate comparable tree recruitment patterns, (b) if legume trees facilitate greater woody species recruitment than non-legume trees and (c) the effect of bird species on germination and regeneration patterns. These results support other findings that plantations facilitate regeneration in various conditions and regions and further suggest that forest managers can influence understory development trajectories by selecting plantation trees of particular species or with particular structural characteristics (Carnevale and Montagnini, 2002; Fimbel and Fimbel, 1996; Healey and Gara, 2003; Holl et al., 2000; Howlett and Davidson, 2003; Lamb, 1998; Loumeto and Huttel, 1997; McClanahan and Wolfe, 1993; Michelsen et al., 1996; Otsamo, 2000; Parrotta, 1992; Powers et al., 1997; Reay and Norton, 1999; Zimmerman et al., 2000).

Acknowledgements

The authors would like to thank the Division of Environment, Sanitation and Security of the ACP, particularly Roy Phillips, for providing site information, access and support. Rick Condit, Oswald Schmitz, George Angehr and David Skelly provided valuable input in study design and analysis. We would also like to thank Georgina Cullman for her assistance in the field and Mark Ashton for providing critical reviews of earlier drafts. This paper is a scientific contribution of the Native Species Reforestation Project (PRORENA) and was generously supported by grants from the Yale Tropical Resources Institute and the Panama Canal Authority.

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