

Barriers to forest regeneration of deforested and abandoned land in Panama

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Summary

1. In Panama, abandoned agricultural lands that supported tropical rain forest are invaded by the exotic invasive grass *Saccharum spontaneum*, which precludes native forest regeneration. This study aimed to evaluate the importance of several barriers to forest regeneration and highlight mitigation opportunities.

2. We examined four barriers to natural regeneration: *Saccharum* competition, seed dispersal limitation, fire and soil nutrient deficiency. Tree and shrub regeneration was measured in a factorial experiment combining *Saccharum* cutting treatments, distances from adjacent forest and a prescribed burn to assess the first three barriers, respectively. We compared soil nutrients in *Saccharum* plots with those from adjacent forest. Additionally, we determined the importance of distance to remnant vegetation (large-leaved monocots, shrubs and isolated trees) on forest regeneration.

3. Fire significantly decreased plant species richness of forest regeneration. Fire inhibited the germination of most species; the effect was exacerbated by cutting the *Saccharum*.

4. Grass competition significantly decreased seedling growth, while soil nutrient deficiency did not affect forest regeneration.

5. Seed dispersal limitation affected density and species richness. Significantly more species (3×) regenerated at 10 m compared with 35 m from the forest. Mean seedling densities were, respectively, four, three and two times higher under large-leaved monocots, isolated trees and shrubs than in open *Saccharum*. When seed input was experimentally equalized, large-seeded species had the highest establishment rate, suggesting that if their propagules were dispersed to the site they would regenerate in high proportions. However, under natural conditions they regenerated poorly and represented the most dispersal-limited species group.

6. *Synthesis and applications.* Our results suggest that facilitation of natural regeneration may be a feasible, low-cost management option for restoring native forest cover to large areas. Firebreaks must be established to promote biodiversity of forest regeneration. We do not recommend *Saccharum* cutting or fertilization as site treatments. Shading effectively eliminates *Saccharum*. Planting a variety of tree species in clumps throughout the *Saccharum* may overcome dispersal limitations and catalyse natural regeneration. Trees that attract different frugivores are recommended, especially large-seeded forest species.

Key-words: abandoned agriculture, natural regeneration, old-field succession, *Saccharum spontaneum*, secondary succession, seed dispersal, tropical forest

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Introduction

Deforestation in the neotropics and subsequent non-sustainable land use has produced vast areas of degraded land. Once abandoned, forest regeneration is often delayed (Uhl, Buschbacher & Serrão 1988; Aide *et al.* 1995). Research throughout the neotropics has shown that a number of factors, often interacting, may impede tropical forest regeneration at deforested, abandoned sites. These include seed dispersal limitations, grass competition, fire, drought and low soil nutrient availability. Insufficient seed dispersal is a major limitation to natural regeneration at many neotropical sites (Uhl, Buschbacher & Serrão 1988; Aide & Cavelier 1994; Holl 1999; Holl *et al.* 2000; Wijdeven & Kuzee 2000; Zimmerman, Pascarella & Aide 2000). The majority of tropical tree species have animal-dispersed fruits (Howe & Smallwood 1982) but most animals, especially large mammalian frugivores (Chapman & Chapman 1999), will not enter far into these deforested areas (Cardosa da Silva, Uhl & Murphy 1996). Wind-dispersed seeds may arrive in high numbers; however, they are often small-seeded and microsite limited, with consequent low establishment rates. For example, Ingle (2003) found that the stem density of vertebrate-dispersed species outnumbered wind-dispersed species, despite the fact that 15 times more wind-dispersed seeds arrived into abandoned areas. Seed dispersal limitation is especially severe for large-seeded species because the predominant seed vectors in abandoned areas (small birds and bats) carry small seeds (Nepstad *et al.* 1996). These limitations can potentially be alleviated when remnant trees (Guevara, Purata & Van der Maarel 1986; Guevara & Laborde 1993; Carrière *et al.* 2002), shrubs (Vieira, Uhl & Nepstad 1994; Holl 2002) and large-leaved monocots (Duncan & Chapman 1999) are present because they attract seed dispersers and facilitate native rain forest regeneration under their canopies.

Deforested and abandoned sites in central Panama are often invaded by a tall (2–5 m) non-native grass species *Saccharum spontaneum* L. ssp. *spontaneum* that grows in dense, impenetrable stands. It has been postulated that *Saccharum* halts natural forest regeneration (Aide & Cavelier 1994) but experimental evidence is lacking (but see Hooper, Condit & Legendre 2002; Hooper, Legendre & Condit 2004). Exotic grasses limit tree regeneration by competing with tree seedlings for water and nutrients (Nepstad 1989; Nepstad *et al.* 1996). Grass invasion also increases the likelihood of fire that in itself further arrests natural forest regeneration in abandoned, deforested lands (Nepstad, Uhl & Serrão 1990). Fire can also impoverish soils, reducing seedling growth (Aide & Cavelier 1994) and impeding forest recovery (Buschbacher, Uhl & Serrão 1988).

The objective of this research was to investigate the relative importance of different factors limiting forest regeneration at deforested sites in Panama that have been invaded by *S. spontaneum* (hereafter *Saccharum*) and test management tools for overcoming these barriers.

We tested the hypotheses that limited seed dispersal, *Saccharum* competition, fire and low soil nutrients are barriers to forest regeneration, while remnant vegetation found in these *Saccharum* grasslands (trees, large-leaved monocots and shrubs) facilitates regeneration. Tree and shrub sprouts, seedlings and saplings were monitored over a 1-year period beginning in August 1996. The effect on regeneration of distance from the forest edge was assessed to evaluate the role of potential seed dispersal limitation. Competition with *Saccharum* was studied by comparing cut and uncut treatments. The effect of fire was investigated by performing a prescribed burn during the dry season. The effect of soil nutrients was assessed by comparing soil nutrients in *Saccharum*-dominated sites and adjacent forest. To determine the effect of remnant vegetation, we recorded the location of each isolated tree, shrub and large-leaved monocot (*Musa* and *Heliconia* spp., which we refer to throughout the text as large monocots) and measured their proximity to each regenerating tree and shrub seedling.

Materials and methods

STUDY SITE

Las Pavas (9°06'N, 79°53'W) is located near the Panama Canal, 4 km south-west of the Barro Colorado Nature Monument (BCNM), where the Smithsonian Tropical Research Institute reserve is located. Prior to deforestation, the study area supported a tropical moist forest similar to the BCNM (Croat 1978). Deforestation began in 1976 (Penna Franco 1990) and by 1984 most of the area had been converted to subsistence agriculture. Agriculture was abandoned before 1990; the site was subsequently invaded by *Saccharum*. The site is moderately hilly and dissected by small streams. Interspersed within the *Saccharum* are isolated trees, shrubs and large monocots and also patches of forest that were spared during deforestation, especially in corridors along streams.

Rainfall at the BCNM averages 2600 mm year⁻¹, with a dry season from mid-December until mid-April (Windsor 1990). During the first wet season of the study (1996), rainfall was above average, but during the 1997 dry season rainfall was well below average (Smithsonian Environmental Sciences Project, unpublished data). Soils are oxisols (Cavelier 1992).

EXPERIMENTAL DESIGN

Five sites, located 0.6–3.4 km apart and in areas dominated by *Saccharum*, were selected. Each *Saccharum*-dominated site was located adjacent to a different forest patch. At each site, we extended a transect into the *Saccharum*, perpendicular to the forest edge; plots were located with midpoints at 10, 35 and 85 m along this transect. Each plot was divided into three 12 × 12-m subplots for the three treatments: cutting the *Saccharum*

once, cutting three times and control (no cutting), with the location of each treatment selected randomly. The *Saccharum* was cut manually with machetes in July 1996 (once cut) and additionally at intervals 4 months apart in November 1996 and March 1997 (thrice cut). The subplots were subdivided into 25 2 × 2-m subsubplots with a 0.5-m trail between them to facilitate seedling measurement and cutting the *Saccharum* without damaging the regenerating vegetation. All tree and shrub seedlings, and saplings found within these plots, were identified to species, tagged and mapped. Origin as root-sprout was recorded whenever possible (we had difficulty determining origin in fewer than 2% of the seedlings). Measurements of height (soil surface to apical meristem) and basal diameter (3 mm above soil surface) were taken for each individual at four regularly spaced census intervals: August 1996 (mid-wet season), December 1996 (end of wet season), April 1997 (late dry season) and mid-July 1997 (early wet season).

To study the effect of fire on tree species regeneration, we repeated the experimental design as detailed above at each site 20–50 m from the pre-existing experimental plots, and established a 15-m firebreak between the two sets of plots (Hooper, Legendre & Condit 2004, electronic appendix B). Plots on one side of the firebreak were left unburned, while plots on the other side were subjected to a prescribed burn during April 1997 (peak fire season). At each site, all plots were surrounded by a 20–25-m firebreak. Despite the large firebreaks, uncontrolled anthropogenic fires crossed the firebreaks at three sites after the third census. Details are provided whenever this affected subsequent statistical analyses. All prescribed burns were successful. Tree seedlings, shrub seedlings and saplings found within these plots were monitored for a year at four census intervals (two pre-fire and two post-fire) following the same methodology and timing as for the unburned plots.

To determine the effect of remnant vegetation on natural regeneration, we located and mapped all shrubs, large monocots and isolated trees and measured their distance from each seedling. We compared invasion success independent of seed rain (data from a companion experiment) to actual occurrences of natural-regenerating species (data from the present study), as done by De Steven (1991), to determine the effect of limited seed dispersal on forest regeneration. In the companion experiment (Hooper, Condit & Legendre 2002), we planted 15 000 seeds of 20 tree species varying in seed size and shade tolerance in equivalent densities 10 m from the present study.

SOIL ANALYSES

Soil samples were taken from the top 20 cm of soil at each experimental subplot located 10 m from the forest patch and also from the top 20 cm of soil in the forest patch adjacent to each subplot, at each site. By comparing grassland and forest soils within 10 m of each other, we attempted to minimize differences in parent

material. Large organic matter was removed and the samples were sieved, ground and pooled for each site. Soil pH was determined using a 1 : 2 soil-to-solution ratio using water (Hendershot, Lalonde & Duquette 1993). Percentage carbon was measured using a wet oxidation of organic matter with an acid dichromate solution heated at 150 °C for 45 min. Organic carbon was estimated by back titration using an indicator of the remaining dichromate with a ferrous ammonium sulphate solution. Available phosphorus, calcium, magnesium, potassium, copper, zinc, manganese and iron were extracted using the Mehlich III solution (Tran & Simard 1993), and analysed by atomic absorption spectroscopy (Perkin-Elmer 5380, Norwalk, CT, USA), except for phosphorus which was determined using a calorimetric technique (flow injection analysis, Lachat Instrument, Loveland Colorado, USA). Extractable ammonium and nitrate were determined using a 1-M KCl extraction with a 1 : 10 soil-to-solution ratio that was shaken for 1 h. The filtrate was analysed by calorimetric determination (Maynard & Kalra 1993). Total nitrogen was determined following digestion in a mixture of K₂SO₄, CuSO₄ and Se (in a ratio of 100 : 10 : 1) and H₂SO₄ at 350 °C for 3 h. The volume was made to 100 mL and the solution was measured calorimetrically (McGill & Figueiredo 1993).

STATISTICAL ANALYSES

For each soil nutrient, a one-way analysis of variance (ANOVA) was computed to compare forest soils with those of experimental subplots in the *Saccharum* grassland. A second ANOVA was computed to compare soils in burned and unburned *Saccharum*.

A two-way split-plot ANOVA with repeated measures was used to test for the effect of distance from the forest, *Saccharum* treatment and time on the number of naturally regenerating individuals, number of species, number of recruits, percentage recruitment, number of root sprouts, percentage root sprouts, number of individuals that survived and percentage survivorship (calculated for each 12 × 12-m subplot). All measurements were transformed to achieve normality prior to statistical analysis. We used a similar ANOVA model with a split-split-plot design to test for the effect of these factors on growth. Relative growth rate (RGR) per individual was calculated as:

$$\text{RGR} = [\ln(D_x) - \ln(D_{x-1})] / T$$

where D_{x-1} and D_x are measurements of diameter on two consecutive dates, T is the number of days between these dates and \ln is the natural logarithm.

To test for the effect of fire on natural regeneration, we used a three-way ANOVA, with a split-split-plot design using the two sites (replicates) that did not suffer fire damage. We compared the burned to the unburned subplots at each site. The model accounted for the variance of the main plot factor, fire with two levels

(burned, unburned), the subplot factor distance from the forest, the subplot factor, *Saccharum* treatment and all interactions.

For the preceding analyses utilizing ANOVA, we used the GLM procedure in SAS (SAS Institute 1988). Type III sums of squares was used throughout and Tukey a posteriori contrast tests were performed on all variables found to be significant ($P < 0.05$) by ANOVA. A significance level of $P < 0.05$ was used for all post-hoc tests. For all repeated-measures analyses, Mauchly's criterion applied to the orthogonal components was used to test for sphericity ($P < 0.05$); if it was not significant, univariate tests were used; otherwise, multivariate tests were used (SAS Institute 1988).

We used linear regression analyses (Proc GLM; SAS Institute 1988) to determine the effect of proximity to remnant vegetation on total seedling density. Remnant vegetation was grouped into three classes: (i) large monocots; (ii) isolated trees (height > 5 m); (iii) shrubs and saplings (2.5–5 m in height). The presence or absence of each remnant vegetation type per 12 × 12-m subplot was coded as a binary predictor variable (presence 1, absence 0). To determine the effect of proximity to the forest, plots close to the forest (5–15 m) were coded with the binary predictor variable 1, while plots located with their midpoints at 35 or 85 m from the forest were coded as 0. We grouped naturally regenerating species into seven categories according to dispersal characteristics including their primary and (if applicable) secondary dispersal mechanism or vector (R. Foster & R. Perez, personal communication): (i) wind-dispersed, not reproducing in grassland; (ii) wind-dispersed, reproducing in grassland [there was a single species in this group, *Cochlospermum vitifolium* (Willd.) Spreng.]; (iii) ballistic dispersal (explosion); (iv) small bird-dispersed (seed size < 10 mm), this group of plants may also be dispersed by bats and other mammals; (v) bat-dispersed (there was a single species in this group, *Piper marginatum* Jacq., which is known to be exclusively bat-dispersed); (vi) arboreal animal-dispersed (seed size > 10 mm), including dispersal by large birds and arboreal frugivores; (vii) secondarily agouti-dispersed [there was a single species in this group, *Gustavia superba* (HBK) Berg., known to be scatterhoarded by agoutis *Dasyprocta punctata*]. The total seedling and sapling density [$\ln(x + 0.1)$ transformed] within each dispersal category was the response variable. We repeated the above analysis for each dispersal category. A Bonferroni correction was applied to the probabilities computed within each remnant vegetation type.

Results

ABIOTIC FACTORS

Cutting the *Saccharum* significantly decreased its live above-ground biomass, from $4652 \pm 1134 \text{ g m}^{-2}$ (control) to $3205 \pm 523 \text{ g m}^{-2}$ (once cut) and $1308 \pm 205 \text{ g m}^{-2}$ (thrice cut) (Hooper, Condit & Legendre 2002). The

cutting treatments significantly increased light levels recorded 0.5 m above ground (control 2.8% incident, once cut 15.3% incident, thrice cut 39.1% incident) (Hooper, Condit & Legendre 2002).

Total soil nitrogen levels were low (Sanchez 1976) and significantly lower ($F_{[1,7]} = 10.97$, $P < 0.013$) in *Saccharum* grassland ($0.37 \pm 0.03\%$, mean \pm standard error) than in adjacent secondary forest ($0.52 \pm 0.03\%$) (see Appendix S1). However, no significant differences between forested sites and grassland were recorded for the available nitrogen forms, ammonium (NH_4) and nitrate (NO_3). Significantly higher levels of soil phosphorus ($F_{[1,7]} = 8.39$, $P = 0.044$) (burned $0.013 \pm 0.005 \text{ mg g}^{-1}$, unburned $0.004 \pm 0.001 \text{ mg g}^{-1}$) and copper ($F_{[1,7]} = 13.74$, $P = 0.021$) were recorded in grassland after fire. No other micro- or macronutrients differed significantly between grassland and forest, or between burned and unburned grassland. Soil pH levels were high (unburned *Saccharum* 5.85 ± 0.13) for tropical soils (Sanchez 1976); the soils had no iron or aluminium toxicity (see Appendix S1).

In total, 4984 individuals of 80 species were encountered naturally regenerating in the *Saccharum*. Mean basal diameter was 6.0 mm, ranging from 0.1 to 69.1 mm. Mean height was 39.2 cm, ranging from 0.7 to 537.4 cm, with 59 stems greater than 2.5 m. The most common species (total number of individuals) were *Gustavia superba* (1060), *Piper marginatum* (522), *Cochlospermum vitifolium* (400), *Spondias mombin* L. (290) and *Cordia alliodora* (Ruiz & Pavon) 241. Details on species composition is given in Hooper, Legendre & Condit (2004), including a full species list.

Tree and shrub density was lower in the first census (August 1996, 14.7 ± 3.1 individuals 10 m^{-2}) than in all subsequent censuses (repeated-measures ANOVA univariate analysis; $F_{[3,36]} = 20.08$, $P < 0.0001$), where density doubled to tripled depending on the season (dry season April 1997, 28.5 ± 6.1 ; wet season December 1996, 35.4 ± 7.9 , August 1997, 33.7 ± 7.1). Percentage survival was highest in the 1997 rainy season (April–August 1997, $82.8 \pm 3.8\%$) and lowest in the preceding dry season (December 1996–April 1997, $71.7 \pm 5.1\%$) but the differences among all periods were not significant. Recruitment and percentage recruitment were significantly reduced during the dry season (repeated-measures ANOVA univariate analysis; recruitment $F_{[2,24]} = 15.39$, $P < 0.0001$; % recruitment $F_{[2,24]} = 19.47$, $P < 0.0001$), falling from an average of 19.0 ± 5.4 recruits 10 m^{-2} ($55.5 \pm 6.9\%$ of all individuals) in December 1996 to 3.1 ± 0.9 recruits 10 m^{-2} ($15.2 \pm 3.4\%$ of all individuals) in April 1997. Tree seedling RGR was also significantly reduced during the dry season, falling to approximately one-third of the rates recorded in the previous wet season (repeated-measures ANOVA univariate analysis; RGR $F_{[2,150]} = 30.02$, $P < 0.0001$; RGR August–December 1996, $196.4 \pm 12.7\%$ year $^{-1}$; December 1996–April 1997, $60.8 \pm 6.5\%$ year $^{-1}$).

The number of species was significantly affected by distance from the forest, and this effect changed over time (repeated-measures ANOVA univariate analysis, distance–

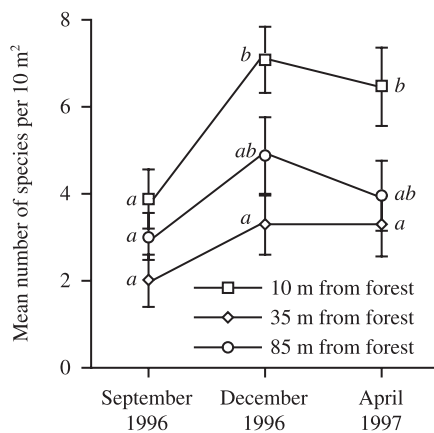


Fig. 1. Effect of distance from the forest on mean number of species per 10 m². The overall effect is significant (ANOVA, distance–time interaction, $P = 0.036$). Similar superscripts indicate no significant ($P < 0.05$) difference following Tukey post-hoc analysis. Means and 1 standard error are presented.

time interaction: $F_{[4,16]} = 3.33$, $P = 0.036$; Fig. 1). The number of species was highest near the forest and lowest at the intermediate distance (35 m). Initially, these differences in species richness were not significantly different but in December 1996 and April 1997 there were significantly more species at 10 m from the forest than at 35 m (85 m was intermediate). To check if these differences in species richness were explained by differences in the number of stems, we used number of stems as a covariate. Although the number of stems did explain a significant portion of richness variation at each sampling time ($P < 0.0001$), the differences in richness remained significantly influenced by distance from the forest in December 1996 ($P = 0.047$) and April 1997 ($P = 0.008$), confirming the results shown in Fig. 1.

RGR of seedlings was significantly higher (ANOVA $F_{[2,4]} = 12.87$, $P = 0.018$) in the thrice-cut *Saccharum*. It averaged $71.8 \pm 6.9\%$ year⁻¹ (thrice cut), $34.1 \pm 5.1\%$ year⁻¹ (once cut) and $25.48 \pm 9.43\%$ year⁻¹ (uncut). No other response variables were significantly affected by distance from the forest or *Saccharum* treatment.

Fire significantly ($F_{[1,4]} = 5.96$, $P = 0.025$) decreased the number of species, from 6.2 ± 0.9 10 m⁻² pre-fire to 2.8 ± 0.6 10 m⁻² post-fire. *Saccharum* mowing treatment significantly altered the effect of fire on recruitment from seed (ANOVA treatment–fire interaction; number of recruits $F_{[2,4]} = 4.43$, $P = 0.027$; percentage recruitment $F_{[2,4]} = 4.88$, $P = 0.020$). Percentage recruitment after fire significantly decreased when the *Saccharum* was cut three times yearly, whereas it increased after fire when the *Saccharum* was cut once or left uncut (Fig. 2). The number of recruits dropped when the *Saccharum* was cut three times, while it increased in the control. There was no significant difference between the number of individuals before and after fire when all seedlings regardless of origin were included in the analysis, but when root sprouts were excluded from the analysis fire reduced average seedling density from 28.2 ± 8.1 10 m⁻² to 11.6 ± 4.3 10 m⁻² (ANOVA $F_{[1,4]} = 4.19$, $P = 0.055$). The

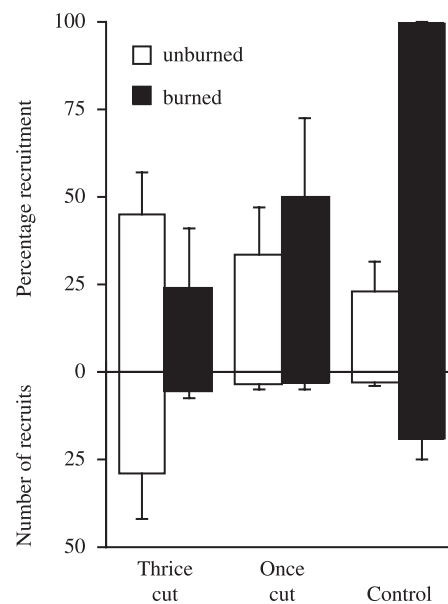


Fig. 2. Effect of fire on percentage and number of recruits from seed (per 10 m²).

percentage of seedlings originating as root sprouts significantly ($F_{[1,31]} = 5.40$, $P = 0.036$) increased in burned plots (unburned $31.3 \pm 7.3\%$, burned $51.8 \pm 10.2\%$).

Large monocots had a significant positive effect on the overall number of individuals (linear regression, $P = 0.014$; monocot absent, 12.2 ± 1.8 10 m⁻²; monocot present, 52.1 ± 14.4 10 m⁻²; Table 1). When species were grouped into categories according to their dispersal mode/vector, we found that plots with a large monocot present had significantly more bat- and agouti-dispersed species ($P < 0.0001$; Table 1). Plots with shrubs and/or saplings had more large arboreal animal- and agouti-dispersed species ($P = 0.010$, $P = 0.040$, respectively). Plots closest to the forest patch had significantly more wind-dispersed species ($P = 0.010$), and plots containing an isolated tree had significantly more ballistically dispersed species ($P < 0.0001$).

When seed input was experimentally equalized, large-seeded shade-tolerant species had the highest germination and survival in the *Saccharum* control (Table 2), whereas small-seeded species performed poorly (Hooper, Condit & Legendre 2002). In contrast, small-seeded moderately light-demanding species naturally regenerated in the highest proportions, while large-seeded shade-tolerant species did not predominate. Large-seeded moderately light-demanding species were found in fairly high proportions (23% of all individuals), yet they belonged to only three species, with a single species (*Gustavia superba*) comprising most of the individuals.

Discussion

A number of factors pose significant barriers to forest regeneration in abandoned agricultural land in Panama, including lack of propagules, seasonal drought, competition with *Saccharum* and fire. The density of tree and

Table 1. Results of linear regression analyses showing the effect of proximity to forest and remnant vegetation, including large monocots, isolated trees and shrub/saplings, on density (10 m^{-2}) on all naturally regenerating seedlings, which are then grouped according to their dispersal vector or mechanism (see text) (only significant results are presented for dispersal groups). Mean number of individuals when the forest was far from the plot or when remnant vegetation was absent from the plot (far) was compared with mean number of individuals when the forest was located within 5 m from the $12 \times 12\text{-m}$ subplot or when remnant vegetation was located in the subplot (near) (means ± 1 SE)

| Response variable | Mean ± 1 SE no. seedlings (far) | Mean ± 1 SE no. seedlings (near) | P^\dagger | $F_{[1,88]}$ | R^2 |
|--|-------------------------------------|--------------------------------------|-------------|--------------|-------|
| Explanatory variable: proximity to the forest (within 5 m) | | | | | |
| All seedlings | 14.1 \pm 2.9 | 20.4 \pm 4.5 | NS | 1.61 | 0.02 |
| Wind (not reproducing) | 0.7 \pm 0.2 | 5.1 \pm 2.3 | ** | 11.05 | 0.11 |
| Explanatory variable: presence of large-leaved monocot | | | | | |
| All seedlings | 12.2 \pm 1.8 | 52.1 \pm 14.4 | ** | 10.30 | 0.11 |
| Bat | 0.9 \pm 0.2 | 12.8 \pm 5.0 | ** | 28.83 | 0.25 |
| Agouti | 2.8 \pm 0.6 | 20.7 \pm 8.0 | ** | 24.39 | 0.22 |
| Explanatory variable: presence of isolated tree (height > 5 m) | | | | | |
| All seedlings | 14.9 \pm 2.4 | 37.8 \pm 17.4 | NS | 3.44 | 0.04 |
| Ballistic | 0.3 \pm 0.1 | 10.2 \pm 5.7 | ** | 18.47 | 0.17 |
| Explanatory variable: presence of shrub/sapling (height 2.5–5 m) | | | | | |
| All seedlings | 12.9 \pm 2.7 | 22.3 \pm 4.8 | NS | 7.37 | 0.08 |
| Large arboreal animal | 1.3 \pm 0.2 | 3.2 \pm 0.6 | ** | 11.04 | 0.11 |
| Agouti | 3.5 \pm 1.5 | 6.5 \pm 1.6 | * | 8.27 | 0.09 |

All response variables are $\ln(x + 0.1)$ transformed.

All seedlings, number of all individuals, not grouped into dispersal categories. Wind (not reproducing), number of wind-dispersed species not reproducing in the *Saccharum*. Explosion, number of ballistically dispersed species. Bat, number of *Piper marginatum* (the only species known to be entirely dispersed by bats). Large arboreal animal, number of large bird- or large mammal-dispersed species. Agouti, number of *Gustavia superba* (the only species secondarily dispersed by agoutis

Dasyprocta punctata).

$^\dagger P$, probability after Bonferroni correction (e.g. 0.104×8 tests = 0.832) within remnant vegetation category: * $P < 0.05$; ** $P < 0.01$.

Table 2. Percentage germination (Germ) and survival (Surv) of all seeds planted in the unmown *Saccharum* control (Experimental) compared with mean percentage abundance of tree seedlings naturally regenerating (Natural regeneration). Species were grouped into three seed size and three shade-tolerance classes

| | Experimental † | | | Natural regeneration | | |
|----------------------|-------------------------|---------------|----------------|----------------------|---------------|----------------|
| | > 0.76 | 0.75–0.75 | < –0.76 | > 0.76 | 0.75–0.75 | < –0.76 |
| Shade-tolerance | Pioneer | Gap-dependent | Shade-tolerant | Pioneer | Gap-dependent | Shade-tolerant |
| Seed size | Germ | Surv | Germ | Surv | % total | % total |
| Small (< 0.15 g) | 13 | 35 | 5 | 0 | 21 | 0 |
| Mid-sized (0.15–1 g) | –‡ | –‡ | 16 | 64 | 21 | 50 |
| Large (> 1 g) | 8 | 40 | 21 | 62 | 31 | 72 |
| | | | | | 6 | 23 |
| | | | | | | 7 |

† Reported in table 4 in Hooper, Condit & Legendre (2002).

‡ No data.

shrub regeneration was fourfold, threefold and twofold higher under large monocots, remnant trees and shrubs/saplings, respectively, than in *Saccharum*-dominated areas devoid of remnant vegetation (which we refer to as ‘open’ *Saccharum*). These results concur with findings at other tropical sites, that trees (Guevara, Purata & Van der Maarel 1986; Guevara & Laborde 1993), shrubs (Vieira, Uhl & Nepstad 1994; Aide *et al.* 1995; Holl 2002; but see Zahawi & Augspurger 1999) and large-leaved monocots (Duncan & Chapman 1999) facilitate woody seedling establishment. This could result from an increased probability of dispersal under remnant vegetation compared with grassland, as documented at other sites for trees (Guevara, Purata & Van der Maarel 1986; Guevara & Laborde 1993; Cardoso da Silva,

Uhl & Murphy 1996; Duncan & Chapman 1999; Toh, Gillespie & Lamb 1999; Wijdeven & Kuzee 2000), shrubs (Vieira, Uhl & Nepstad 1994; Holl 2002) and large monocots (Duncan & Chapman 1999). It may also result from a higher probability of seedling establishment under remnant vegetation (Guevara & Laborde 1993; Holl 2002) because of lowered grass competition and a more favourable microclimate (Vieira, Uhl & Nepstad 1994). Research suggests both are necessary to enhance seedling density, as increased seed rain without favourable conditions for seedling establishment does not lead to enhanced recruitment (Holl 1998). Our results suggest that a combination of enhanced dispersal and establishment increases seedling density under remnant vegetation compared with open *Saccharum*.

DISPERSAL

Differences in the relative density of recruitment below different types of remnant vegetation may result from differential attraction to frugivores. Significantly higher densities of mammalian-dispersed species were found below large monocots (agouti- and bat-dispersed seeds) and shrubs/saplings (agouti- and large-arboreal-animal-dispersed seeds) compared with open *Saccharum*. Similarly at other tropical sites, higher densities of animal-dispersed seed rain have been reported under shrubs (Vieira, Uhl & Nepstad 1994; Holl 2002). Species found under remnant vegetation at our site included large-seeded primary forest species. These results suggest that different remnant vegetation types in the *Saccharum* attract different frugivores, increasing the diversity of tree species and the proportion of large-seeded primary forest species regenerating.

We found almost equal numbers of bat-dispersed seedlings compared with small bird-dispersed seedlings. Other neotropical studies have shown that bat seed rain can surpass bird seed rain in degraded areas (Thomas *et al.* 1988; Gorchoff *et al.* 1993). Cardoso da Silva, Uhl & Murphy (1996) found that bats disperse more woody vegetation into areas with few trees and shrubs, whereas small birds contribute more seed rain once trees and shrubs are established; our results concur. The bat-dispersed *Piper marginatum* was often the only species present in open *Saccharum*. However, we recorded more small bird-dispersed species overall, suggesting that birds play a pivotal role in increasing biodiversity during succession.

While the density of naturally regenerating trees and shrubs correlated with proximity to remnant vegetation, it did not correlate with distance to the forest. Duncan & Duncan (2000) and Slocum & Horvitz (2000) similarly found no relationship of distance from the forest with the density of natural regeneration in degraded areas containing remnant vegetation. The effect of distance from the forest may vary with species' dispersal mechanisms and site factors; for example in a temperate system Holl & Crone (2004) found that only wind-dispersed species are affected by distance from the forest, whereas animal-dispersed species are more influenced by site factors. Similarly, in a tropical context distance from the forest has little effect on animal-dispersed seed rain at some sites adjacent to forest that are near isolated trees and shrubs (Guevara, Purata & Van der Maarel 1986; Willson & Crome 1989). These results contrast with findings at other tropical locations that seedling density decreases sharply with increasing distance from the forest edge (Aide & Cavelier 1994), as does seed rain density (Nepstad, Uhl & Serrão 1990; Gorchoff *et al.* 1993; Aide & Cavelier 1994; Holl 1999; Wijdeven & Kuzee 2000) and frugivore abundance (Cardoso da Silva *et al.* 1996). Slocum & Horvitz (2000) suggest that distance from the forest is most important when vegetation such as trees and shrubs are not found in degraded lands, for example during early successional stages, and our results support this conclusion.

Species richness declined significantly with increasing distance from the forest; this is a major barrier to the re-establishment of biodiversity. Species richness was almost threefold lower at 35 m compared with 10 m from the forest; wind-dispersed species (not reproducing in grassland) declined significantly with distance from the forest. Holl (1999) and Aide & Cavelier (1994) report a similar decline in species richness with increasing distance from the forest edge. This may result from dispersal limitations, for example Zimmerman *et al.* (2000) document a negative effect of distance from the forest on species richness of seed rain, and Duncan & Chapman (1999) report a low proportion of forest species in old-field seed rain, despite close proximity to primary forest. At our site, barriers to the re-establishment of biodiversity may be alleviated if remnant vegetation is present. Both distance from the forest and distance from large-leaved monocots significantly and negatively affected species richness, accounting for a large proportion of variation (68.1%) at our site (Hooper, Legendre & Condit 2004). Bat-dispersed and agouti-dispersed species predominated near monocots. Agoutis surpass all other neotropical mammals in dispersing large seeds because of their scatterhoarding behaviour (Hallwachs 1986); our results suggest they play a key role in increasing diversity by hastening the return of large-seeded forest species.

Evidence for insufficient seed dispersal in open *Saccharum*, especially large-seeded species, is suggested when comparing results from a companion study at the same site, where we planted 20 species of native trees varying in seed size and shade-tolerance characteristics (Hooper, Condit & Legendre 2002). When seed input was equalized, large-seeded shade-tolerant species had the highest germination and survival. Yet most naturally regenerating individuals were small-seeded gap-dependent species (Table 2) with low survival. If seed input of the large-seeded shade-tolerant species was not limiting, their higher germination and survival suggest that they would be found in the highest proportions, yet they rarely regenerated. These findings suggest that regeneration of woody species in Panama faces a similar combination of dispersal and physiological constraints to that documented in abandoned Amazonian pastures. Small-seeded bat- and bird-dispersed species are the most likely to be deposited into abandoned Amazonian pastures; however, these species have the lowest survival (Nepstad *et al.* 1996). At our site, a notable exception to this trend was that 23% of the regeneration was large-seeded gap-dependent seedlings. However, as the majority of these seedlings were a single species (the agouti-dispersed *Gustavia superba*), limited seed dispersal of large-seeded species remains a concern because it constrains biodiversity of naturally regenerating forests.

ESTABLISHMENT

While results reported in the present study do not address whether establishment success is enhanced under remnant vegetation, related research at this site shows that tree

seedlings establishing in shaded conditions with no *Saccharum* have enhanced performance compared with those found in sites colonized by *Saccharum*; *Saccharum* competition (both above- and below-ground) negatively affected the performance of most naturally regenerating woody species (Hooper, Condit & Legendre 2002).

The density, recruitment and growth of naturally regenerating trees and shrubs in open *Saccharum* were significantly reduced during the dry season, suggesting that drought limits natural regeneration at our sites. Research in Brazil has shown that higher temperatures and lower soil moisture availability in abandoned pastures compared with tree-fall gaps causes water stress for plants, limiting their establishment and survival (Nepstad *et al.* 1996). Fruit availability during the dry season may also be lower (Cardosa da Silva, Uhl & Murphy 1996), affecting recruitment.

Physiological stresses are exacerbated when tree seedlings have to compete with grasses for soil moisture and nutrients (Nepstad 1989). Removal of above-ground grass biomass can be detrimental to seedling germination and survival as a result of hotter, drier conditions at the soil surface (Zimmerman *et al.* 2000), especially during the dry season (Hooper, Condit & Legendre 2002). However, grass removal can enhance seedling growth (Ganade & Brown 2002), especially growth of light-demanding species (Hooper, Condit & Legendre 2002). In the present study we found that seedling relative growth rates were three times higher in mown compared with unmown treatments, reflecting the high proportion of moderately (58%) to highly (25%) light-dependent seedlings regenerating at our site.

FIRE

Fire was a major barrier to native tree regeneration because it decreased species richness; species richness was more than twice as high in unburned compared with burned plots. In contrast, the density of regenerating tree and shrub species was not significantly affected by burning because a subset of the original species resprouted in high densities after fire (Hooper, Legendre & Condit 2004; also reported in Australia Setterfield 2002). Burning reduces the number of species resprouting at other tropical sites (Uhl *et al.* 1990; Sampaio, Salcedo & Kauffman 1993). Fire severity significantly affected the recruitment of individuals originating from the seed bank. Recruitment from the seed bank was higher after fire when the *Saccharum* was left unmown and lower if it was mown prior to burning. Mowing the *Saccharum* resulted in a large amount of highly flammable *Saccharum* litter on the ground. This may have increased the temperature of the fire and decreased the size of the viable seed bank (Uhl *et al.* 1981).

SOIL NUTRIENTS

We found no conclusive evidence that soil nutrients were a barrier to natural regeneration of tree and shrub

species. While total nitrogen was significantly lower in grassland compared with adjacent forest, no significant differences between forested sites and grassland were recorded for the available nitrogen forms ammonium (NH₄) and nitrate (NO₃). We recommend a more precise analysis of available nitrogen because we used dry soil samples, in which some available nitrogen may have been lost. At forested sites 7 km from our study area, Cavelier (1992) reported similar values of total nitrogen as those we report in grassland, further suggesting that recorded soil nutrient levels were sufficient for forest development.

CONCLUSION

Facilitation of natural regeneration may be a feasible, low-cost management option for restoring native forest cover to large areas in Panama invaded by *Saccharum*. Firebreaks must be established to promote biodiversity of forest regeneration, as species richness significantly declined following fire. Even with the removal of fire, natural tree regeneration will not proceed unassisted, especially if the desired goal is to restore a species composition similar to primary forest (Hooper, Legendre & Condit 2004). Low seed dispersal limits regeneration of large-seeded species, while small-seeded species are constrained by *Saccharum* competition. Shading effectively eliminates *Saccharum* and enhances tree regeneration (Hooper, Condit & Legendre 2002), suggesting that planting trees to overcome dispersal limitations and produce a shade cover is the best way to eliminate *Saccharum*. We suggest planting a variety of tree species in clumps throughout the *Saccharum* to catalyse natural regeneration, in a process similar to the nucleation model of regeneration of Yarranton & Morrison (1974); similar recommendations have been proposed at other tropical sites (Nepstad, Uhl & Serrão 1990; Lamb *et al.* 1997). Trees that attract a spectrum of frugivores are recommended (Martinez-Garza & Howe 2003), especially large-seeded forest species, as they have the highest performance in the *Saccharum*. Tall tree species with a high crown density should be considered, as they promote bird dispersal (Jones *et al.* 2004); this may increase diversity. Planting shrubs and large monocots would further increase diversity by attracting bats and agoutis. We do not recommend costly *Saccharum* cutting treatments because they did not significantly increase density, species richness or survival of forest regeneration. As cutting did increase seedling growth, it may be suitable for small-scale intensive forest restoration. Burning or fertilization of the regeneration site would not be cost-effective, as fire decreased regeneration from the seed bank, and soil nutrients did not limit seedling establishment.

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Supplementary material

The following supplementary material is available for this article online.

Appendix S1. Soil analyses: results of ANOVA for each element comparing unburned forest with unburned soils in *Saccharum* grassland.