

Forest Regeneration from Pasture in the Dry Tropics of Panama: Effects of Cattle, Exotic Grass, and Forested Riparia

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Abstract

We currently have the opportunity to restore one of the most threatened tropical ecosystems on the Pacific coast of Panama as a consequence of land use change. Factors that influence succession must be understood in order to capitalize on natural regeneration mechanisms. In this study, we determined the effects of exotic grass removal, cattle removal, proximity to forested riparian zones, and topography (upslope vs. downslope) on the initial stages of forest regeneration from pasture in a dry tropical region. After 3 years, basal area, stem density, and species richness of plants (trees, shrubs, vines, and herbs) were significantly and positively affected by exclusion of cattle, presence of exotic grass (no herbicide application), and presence of adjacent forested riparian zones ($p < 0.01$). Interactions between factors were not significant. Cattle foraged and

stomped on vegetation, whereas herbicide application, although effectively removing grass, also killed tree and shrub sprouts, the major source of regrowth. Proximity to forested riparian zones had the greatest effect on species diversity. Shannon's index for diversity (H) equaled 3.23 in plots adjacent to forested riparian zones as compared to 2.78 in plots not associated with these areas. Our recommendations during the early stages of forest succession are to (1) exclude cattle, (2) make site-specific decisions about herbicide application based on the presence or absence of forested riparia and prevalence of coppicing, and (3) actively conserve and protect riparian zones, which function as a critical source of diverse propagules.

Key words: *Guazuma ulmifolia*, herbicide, natural regeneration, rehabilitation, riparian, tropical dry forest.

Introduction

Land use practices are changing in Central America from a combination of declining productivity of cattle pastures (Maass 1995; Mooney et al. 1995) and increasing land value, particularly along the Pacific coast. Dry tropical forest regions have historically been a desirable place to live due to the climate (less rainfall) and lower incidence of disease (e.g., malaria) (Murphy & Lugo 1986). Much of the Pacific coast was dry tropical forest before the land was cleared for cattle (Janzen 1986; Sabogal 1992), beginning with the arrival of the Spaniards in the fifteenth century (Murphy & Lugo 1995) and followed by pasture expansion in the early twentieth century (Maass 1995). The remaining dry tropical forest represents a small fraction of their original forest in Central America, reported as 2% of their original area in 1986 (Janzen 1986; Murphy & Lugo 1995).

In the twenty-first century, the land is again in a state of transition from pasture to abandonment or active reforestation. Consequently, there is an opportunity to restore one of the least known and most threatened tropical eco-

systems (Janzen 1988; Bullock 1995; Mooney et al. 1995; Gillespie 1999; Sanchez-Azofeifa et al. 2005; Vieira & Scariot 2006). Many new landowners are interested in reforesting with native trees to increase biodiversity, forest cover, and long-term economic value. Rehabilitation of dry tropical forest regions may be accomplished by establishing intensive native species plantations or by relying on the natural regenerative capacity of the landscape with limited management (e.g., herbicide application, enrichment planting) (Ashton et al. 1997, 2001; Tomohiro et al. 2006). Factors that facilitate or inhibit forest succession must be understood to effectively capitalize on natural regeneration mechanisms, which can complement the more time- and cost-intensive plantation strategies.

Natural regeneration of abandoned pastures within dry tropical ecosystems is less understood than in better studied temperate and wet tropical forests (Swaine 1992; Mooney et al. 1995; Kennard 2002; Vieira & Scariot 2006). Existing research on dry tropical systems has been based on observational measurements rather than experimental treatments, which are necessary to tease out the underlying factors affecting forest succession (Ewel 1977; Murphy & Lugo 1986; Janzen 1988; Gerhardt 1993; Kennard 2002; Kalacska et al. 2004). The same regeneration barriers may be present within wet and dry tropical ecosystems, such as lack of seed sources, seed predation, plant herbivory, and harsh microclimatic conditions. However,

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species assemblages and functional groups, limiting resources, and land use history may differ. Compared to wet tropical forests, dry tropical forests have a higher dominance of wind-dispersed species (Mooney et al. 1995) and coppicing species (Ewel 1977; Murphy & Lugo 1986); water tends to be the limiting resource rather than nutrients (Frankie et al. 1974; Murphy & Lugo 1986); and pastures are often grazed for a longer period of time.

Cattle have been reported to have both a negative and a positive effect on vegetation. In the wet and dry tropics, excluding cattle from regenerating pastures has been recommended because the animals damage seedlings (Guevara et al. 1986; Guevara & Laborde 1993; Williams-Linera et al. 1998; Harvey & Haber 1999) and compact the soil, increasing soil water run-off and decreasing the availability of water and nutrients (Fleischner 1994; Belsky & Blumenthal 1997). Alternatively, a low density of cattle has been recommended in restoration plans (Janzen 1988; Belsky & Blumenthal 1997; Posada et al. 2000). Cattle disperse seeds with dung that can provide a favorable microclimate (e.g., *Enterolobium* spp., *Guzuma* spp.) (Janzen 1982a, 1982b, 1986, 1988). Cattle may also benefit tree seedlings by foraging on competing grass (Rummell 1951; Janzen 1988; Karl & Doescher 1993; Belsky & Blumenthal 1997; Posada et al. 2000).

Our review of the literature suggests that eradication of grasses may or may not increase available resources to tree seedlings depending upon the site conditions. The dense root systems of grass can outcompete seedlings for moisture and available soil nutrients, and the thick grass canopy may limit light availability during the wet season (Nepstad et al. 1990). Exotic grasses such as *Hyparrhenia rufa* (Nees) Stapf may also perpetuate a fire disturbance regime (Janzen 1988). On the other hand, the removal of grass may increase surface desiccation during the dry season (Knoop & Walker 1985; Gerhardt 1993; Aide & Cavelier 1994; Holl 1999).

Patterns in forest succession may also be influenced by proximity to forested riparian zones and topographic position. Relatively narrow strips of forested riparian zones, an element of some active pastures in the Azuero Peninsula, may serve as a major source of seeds and animal seed dispersers in a landscape devoid of large forest fragments (Nepstad et al. 1990; Gerhardt & Hytteborn 1992; Guevara et al. 1992; Aide et al. 2000). Also, lower slopes are generally more fertile with higher soil moisture than the well-drained upper slopes due to water transport of base cations down slopes (Scatena & Lugo 1995). Thus, regeneration may be higher on lower slopes irrespective of the presence of forested riparian zones.

In order to assess the resilience of a dry tropical forest region after extended pasture use, experimental plots were designed to quantify the effect of (1) cattle, (2) herbicide to kill grass, (3) forested riparian zones, and (4) topography on the early stages of plant succession. Our overarching objective was to determine what species and functional groups of the original forest regenerate as sec-

ond growth after various combinations of treatments. We predicted that species richness, basal area, and stem count would be greater in plots excluding cattle, applied with herbicide, adjacent to forested riparian zones, and on lower slopes.

Methods

Site Description

The study site was located in the dry tropical forest region (Holdridge 1967) of Los Santos province on the Pacific side of Panama (lat 7°15'30"N, long 80°00'15"W). Experimental plots were located near the Achotines Tuna Laboratory, which received 1,300 mm of rainfall in 2002, 1,600 mm in 2003, and 1,500 mm in 2004. The 2002–2004 precipitation total was much lower than the Achotines Laboratory records from 1987 to 1997 where rainfall averaged 1,800 mm annually (unpublished laboratory records), suggesting an overall decline in rainfall and consistent with our communications with local farmers.

The dry season is pronounced with 4 months out of the year receiving little to no rain (December through March). Basalt is the underlying geology, laid down during the Cretaceous era (Instituto Geográfico Nacional Tommy Guardia 1988). The young soils are relatively nutrient rich (cation exchange capacity = 21 meq/100 g). Soil textures range from clay loam to clay (Griscom 2004).

From 1940 to 1950, the original dry tropical forest was transformed into pasture for cattle ranching. The undulating terrain ranges in elevation from 10 to 100 m and is a mosaic of pastures planted with African grasses, forested riparian zones, isolated trees, and live fences. Experiments were conducted in an 85-ha pasture. The land is grazed by a herd of 50–70 Brahman cattle from mid-July until mid-March (approximately 0.6–0.8 head/ha). The land lies fallow for approximately 4 months each year during the late dry season and early rainy season. No fire is intentionally used, although accidental fire, burning portions of the pasture, is an annual occurrence.

Experimental Design

Initially, a global positioning system was used to map out the dimensions of the 85-ha pasture on a georeferenced photograph. Ten riparian zones were located and identified as forested or deforested (dominated by pasture grass). A forested riparian zone was defined as stream with at least one line of trees along each side. Six riparian zones (three forested and three deforested), separated by at least 100 m, were then randomly selected. A seepage way running into each riparian zone was randomly identified. At each of the six site locations, 16 plots (each 9 × 12 m) were located along the seepage way (Fig. 1). Eight plots were located in a “downslope” set starting approximately 10 m up the seepage way from the stream center, and eight plots were located in an “upslope” set

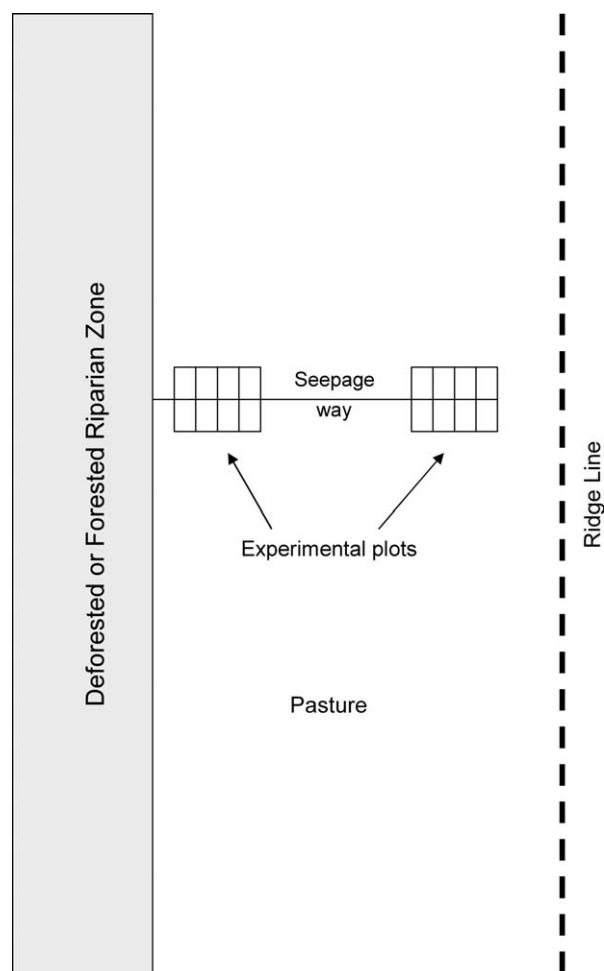


Figure 1. Landscape layout of the experimental plots. Plots (9×12 m) were located along seepage ways adjacent to forested or deforested riparian zones. Eight plots were located in a “downslope,” and eight plots were located in an “upslope” set.

starting approximately 70 m up the seepage way from the stream center. Downslope and upslope sets of plots were separated by 20 m (Fig. 2). The plots ranged in steepness from 16 to 25°. A 2^4 factorial design was constructed where each of the four factors had two levels as follows:

- Herbicide: presence versus absence
- Cattle: presence versus absence
- Riparian zone: forested versus deforested
- Topography: upper slope versus lower slope

Plot locations were initially cleared with machetes of preexisting vegetation during the early wet season (May 2002). In plots excluding cattle, live fences were constructed with stakes and barbed wire. Plots including cattle had the same number of stakes spaced 2 m apart but without wire. This fence design was to control for seed deposition from bird perching. After the cattle fences were constructed, Roundup herbicide (glyphosate) was applied evenly to designated plots (July 2002). Herbicide applica-

tion was repeated 2 months later in September 2002 during the middle of the rainy season. All plots were protected from fire in the dry season by constructing firebreaks.

Plot Measurements of Soil and Light

Light and soil moisture within plots were measured throughout the year. Light quality was determined with ASA 400 hemispherical photography using NIKON FC-E8 fish-eye converter lens fitted to a Nikon Coolpix 950 digital camera. A Delta-T devices mount was used for horizontal leveling and north-south orientation of the camera and lens. Light measurements were taken at 1 m height in the center of each plot during the first wet season (August 2002), the first dry season (February 2003), and the second wet season (August 2003). Measurements were taken at dawn before the sun rose for even sky lighting. The photographs were analyzed with Hemiview software (Delta-T Devices Ltd., Cambridge, U.K.) was used to classify photograph pixels into 2 classes: clear sky or sky obscured by vegetation or land. Hemiview software calculates the global site factor (GSF), which is the proportion of diffuse and direct light striking a point over the amount of light that would strike the same point given no overhead obstructions over the course of a year. The values range from 0 (no light) to 1 (complete light).

For 1 year (October 2003 to November 2004), soil samples were collected to 10 cm depth every 2 weeks in the experimental plots. Percent soil water content was determined using the gravimetric method. Soil samples were

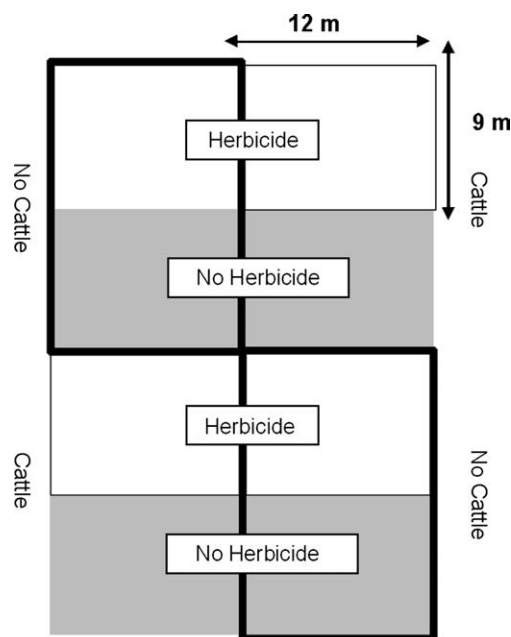


Figure 2. Design of experimental plots (8 of 16 plots shown). This model was replicated six times (three adjacent to forested riparian zones and three adjacent to deforested riparian zones) within an 85-ha pasture in Panama.

initially weighed (wet weight), dried in the oven at 80°C for 7 hours, and weighed again (dry weight). Percent soil water was calculated from the following equation: Soil water (%) = [(wet weight (g) – dry weight (g))/dry weight (g)] × 100.

Natural Regeneration

The percent cover of grass and broad-leaf plants was recorded within eight 1-m² subplots during the first 2 years. In May 2005, a nested plot design was implemented. All plants greater than or equal to 3 cm diameter at breast height (dbh) were quantified in the 9 × 12-m plots. All plants less than 3 cm dbh and greater than 1 m in height were quantified in three 2-m diameter (3.14 m²) subplots (plants <1 m in height were not measured). They were then put into one of the three categories (0–0.9, 1.0–1.9, and 2.0–2.9 cm dbh). Individuals were measured, identified, and when possible categorized as regenerating from seed or sprout.

Statistical Analysis

Data were analyzed using S-Plus software (S-Plus 200 Professional Release 3; Insightful Corporation, Seattle, WA, U.S.A.) as a four factorial, fixed analysis of variance with interaction. Each factor had two levels. The equation was as follows: dependent variable measured (basal area, stem density, species richness) ~ cattle (A) × herbicide (B) × riparian zone (C) × topography (D). All four factors were designated as fixed because two levels were defined in our design (presence vs. absence or in the case of topography, lower slope vs. upper slope) (Searle et al. 1992; Bennington & Thayne 1994). Topography was later removed from the analysis because it did not have a significant effect. Species count, stem count, and basal area followed Poisson distributions and were consequently transformed by taking the square root of the values.

Species diversity was calculated with the Shannon's diversity index ($H' = \sum p_i \log p_i$, where p_i is the fraction of individuals belonging to the i th species) using summed data from all plots of a given treatment. Shannon's equitability (E_H) was calculated by dividing H by $H_{\max}$, where $H_{\max} = \ln S$ and S = the total number of species in the community (richness). Equitability assumes a value between 0 and 1 with 1 being complete evenness. We did not statistically compare Shannon diversity or evenness between treatments due to the limited number of replicates and relatively high diversity of this system because these indices are intended for larger sampling levels particularly for diverse systems (Magurran 1988).

Results

Initial Successional Trends (0–16 Months)

There was a significant difference in light (GSF) and soil moisture within plots. Plots adjacent to riparian zones had

consistently lower light and lower soil moisture conditions (Table 1). Herbicide application initially increased light levels and decreased soil moisture in the experimental plots during the first growing (wet) season. Soil moisture continued to be significantly lower in herbicided plots during the dry season. Cattle significantly increased light during both wet seasons but had no effect on soil moisture.

In the first 3 months, herbicided plots had less vegetation cover (43%), which was equally composed of broad-leaf and grass species. Non-herbicided plots had significantly more vegetation cover (99%), which was dominated by the exotic grass *Hyparrhenia rufa* (Nees) Stapf and *Panicum maximum* Jacq. (87%). Both species attained heights of over 2 m during the wet season. After 16 months, the percentage of grass cover to broad-leaf cover was similar in herbicided and non-herbicided plots with grasses representing on average 25% and broad-leaf species representing 75% of the vegetation.

Successional Trends After 3 Years

Dominant Species. After 3 years, a total of 69 plant species greater than 1 m in height were found within experimental plots (Appendix). At this time, few tree species had individuals with a dbh greater than six cm (Fig. 3). *Guazuma ulmifolia* (Sterculiaceae) had the greatest stem density (34% of all plant stems) and basal area (42% of all plant basal area). Six species represented an additional 30% of the total number of stems: *Clibadium* sp. (Compositae), *Bauhinia* sp. (Leguminosae), *Sida* sp. (Malvaceae), an unidentified species in the Scrophulaceae family, *Vernonia* sp. (Compositae), and *Cordia alliodora* (Boraginaceae) (Appendix). By basal area, *Pouteria campechiana* (Sapotaceae), a stump-sprouting understory tree, was the second most dominant species followed by the light-demanding tree species, *Trema micrantha* (Compositae), and shrubs, *Clibadium* sp., *Vernonia* sp., and *Bauhinia* sp.

Regeneration Modes. Of the species that regenerated by seed, 50% were dispersed by wind or explosive mechanisms (e.g., *Hura crepitans* [Euphorbiaceae]) and 50% were dispersed by animals, mostly birds and bats (e.g., *Acacia collinsii* [Leguminosae], *Cecropia peltata* [Cecropiaceae]). Common tree species regenerating exclusively by seed were *T. micrantha*, *Astronium graveolens* (Anacardiaceae), *C. peltata*, and *H. crepitans*. Of these four species, only *C. peltata* was dispersed by animals. Common tree species regenerating by coppicing were *G. ulmifolia*, *Annona purpurea* (Annonaceae), and *Cochlospermum vitifolium* (Cochlospermaceae). We were not able to quantify precisely the ratio of regeneration from seed versus coppicing due to the difficulty of differentiating the two in every case. However, we estimated that coppicing was about twice as common as regeneration from seed.

Experimental Treatment Effects. After 3 years, basal area, stem density, and species richness were positively

Table 1. Means given for light levels quantified by GSF, and soil moisture percent quantified by percent water content within experimental plots.

	Wet Season		Dry Season		Wet Season	
	Light	Soil Moisture	Light	Soil Moisture	Light	Soil Moisture
Riparian Zone						
–	0.90 (0.1)	19.8 (2.0)	0.94 (0.03)	9.61 (1.5)	0.83 (0.16)	21.21 (2.7)
+	0.84 (0.13)	19.7 (1.8)	0.92 (0.03)	8.80 (1.2)	0.73 (0.16)	18.82 (1.9)
<i>F</i>	22.5	0.01	26.4	12.61	19.7	31.59
<i>p</i>	0.0001	n.s.	0.0001	0.001	0.00001	0.0001
Cattle						
+	0.89 (0.12)	19.6 (1.9)	0.94 (0.03)	9.14 (1.3)	0.84 (0.14)	19.92 (2.3)
–	0.84 (0.13)	19.9 (1.8)	0.93 (0.04)	9.27 (1.5)	0.71 (0.17)	20.11 (2.9)
<i>F</i>	12.2	0.85	3.1	0.3	28.8	0.21
<i>p</i>	0.001	n.s.	n.s.	n.s.	0.0001	n.s.
Herbicide						
+	0.93 (0.04)	19.4 (1.8)	0.93 (0.04)	8.97 (1.3)	0.75 (0.19)	19.81 (2.6)
–	0.79 (0.14)	20.1 (1.9)	0.93 (0.03)	9.44 (1.4)	0.79 (0.14)	20.21 (2.7)
<i>F</i>	89.6	5.13	0.05	4.29	1.61	0.89
<i>p</i>	0.0001	n.s.	n.s.	0.05	n.s.	n.s.

Grand means are given for three seasons: the first wet season, the first dry season, and the following wet season. Standard errors are in parentheses. Significance of factors on measured variables was determined by multifactor analysis of variance. (+), presence of the factor; (–), absence of factor. Topography (+), upper slope; (–), lower slope. n.s., not significant. Interactions were not significant and are therefore not reported. Degrees of freedom equaled 1 for all factors.

affected by cattle exclusion, no herbicide application, and proximity to a forested riparian zone ($p < 0.01$; Fig. 4, Table 2). Interactions were not significant. Topography had no effect on any measured variables and was removed as a main effect.

The exclusion of cattle had a significant, positive effect on basal area ($0.026 \text{ m}^2/100 \text{ m}^2$) and stem density (19 stems/ 100 m^2) compared to plots with cattle, which had an average basal area of $0.013 \text{ m}^2/100 \text{ m}^2$ and stem density of 10 stems/ 100 m^2 . The presence of cattle increased light in the wet season (Table 1), but this potential positive effect

did not balance out the negative impact of cattle on stem density and basal area. Species diversity and evenness (Shannon's index) was similar in plots with and without cattle ($H = 3.22$, $E_H = 0.76$ with cattle; $H = 3.10$, $E_H = 0.73$ without cattle).

Herbicide application increased light significantly in the wet season, decreased soil moisture, and killed all coppice regeneration (Table 1). After 3 years, herbicide application had an unequivocal, negative effect with lower number of stems (11 stems/ 100 m^2) and lower basal area ($0.014 \text{ m}^2/100 \text{ m}^2$) than non-herbicide plots, which had a stem density of 18 stems/ 100 m^2 and basal area of $0.026 \text{ m}^2/100 \text{ m}^2$. The largest stems were found in non-herbicide plots because they all, except for *C. peltata*, regenerated by coppicing (Fig. 3). The six species with stems greater than 8 cm dbh within non-herbicide plots were the following: *Cordia* sp. ($n = 1$), *G. ulmifolia* ($n = 3$), *C. peltata* ($n = 2$), *Co. vitifolium* ($n = 1$), and *P. campechiana* ($n = 1$). However, species diversity and evenness (Shannon's index) was positively affected by herbicide application ($H = 3.23$, $E_H = 0.76$ in herbicide plots; $H = 3.00$, $E_H = 0.70$ in non-herbicide plots).

Plots associated with forested riparian zones had significantly greater stem density (17 stems/ 100 m^2 vs. 11 stems/ 100 m^2) and basal area ($0.023 \text{ m}^2/100 \text{ m}^2$ vs. $0.015 \text{ m}^2/100 \text{ m}^2$) than plots associated with deforested riparian zones. Shannon's index for diversity (H) and evenness was substantially higher for forested plots ($H = 3.23$, $E_H = 0.76$) than for deforested plots ($H = 2.78$, $E_H = 0.65$).

Seven woody species were site specific, defined as species where 90% of the stems were associated with a particular treatment (Table 3). *Annona purpurea* and *Co. vitifolium* only regenerated where herbicide had not been applied. Conversely, *T. micrantha*, a fast-growing, light-demanding species, regenerated exclusively in herbicide

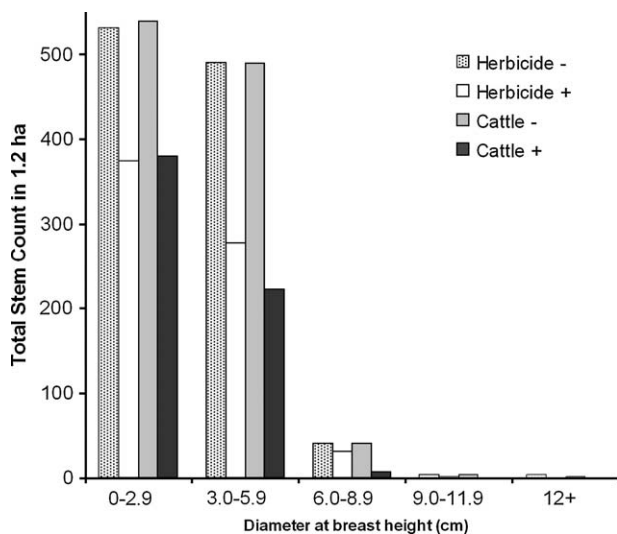


Figure 3. Total stem count of natural regeneration by dbh (cm) after 3 years in experimental plots. All plots in each treatment were pooled together. Factors: cattle and herbicide; (+), presence of the factor; (–), absence of factor.

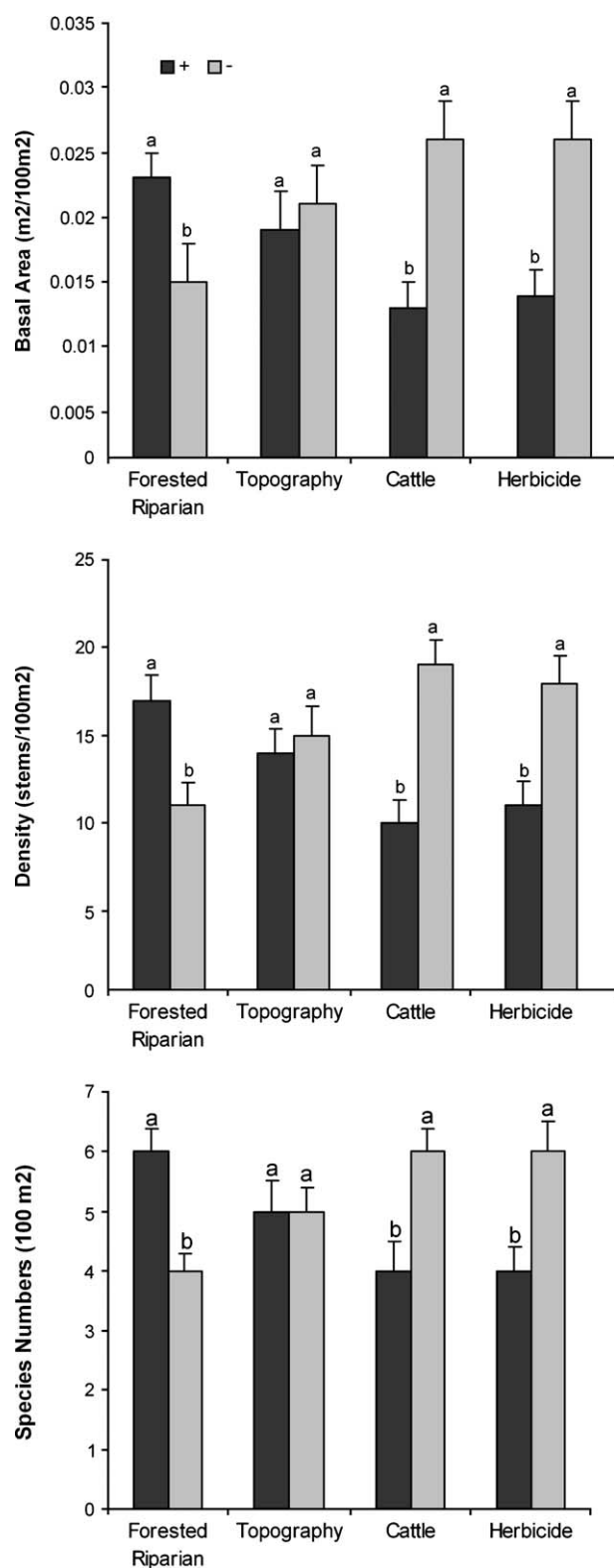


Figure 4. Mean basal area ($\text{m}^2/100 \text{ m}^2$), density (stems/ 100 m^2), and species number (100 m^2) of natural regeneration greater than 1 m in height in experimental plots. (+), presence of the factor; (-), absence of factor. Topography (+), upper slope; (-), lower slope. Significance ($p < 0.05$) are assigned by letters between the two groups: a > b.

plots, and this species in addition to *Vernonia* sp. and *Muntingia calabura* (Elaeocarpaceae) were of considerable size (between 8 and 10 cm dbh) after 3 years in this treatment. Two tree species occurred only when cattle had been excluded, suggesting that they may have been preferred forage species: *T. micrantha* and *Co. vitifolium*. Five tree species were strongly associated with forested riparian zones: *A. purpurea*, *As. graveolens*, *Calycophyllum candissimum*, *C. peltata*, and *Co. vitifolium*.

Discussion

Coppicing is the primary mechanism of regeneration within abandoned pasturelands of dry forest regions (Ewel 1980; Murphy & Lugo 1986; Russell-Smith 1996; Kennard 2002; McLaren & McDonald 2003; Vieira & Scariot 2006). The high proportion of coppicing species may be due to inherent selective forces in dry tropical systems and/or selective pressure from over 50 years of intensive pasture in the landscape. Human disturbance regimes of fire and cattle select against species that are not capable of this regeneration strategy.

Guazuma ulmifolia is a prolific stump sprouter and the most common remnant tree encountered in pasture inventories and within riparian zones (Griscom 2004). Likewise, it was the most common species regenerating from sprout or seed in the experimental plots. This species also dominated early succession in Costa Rica, where it represented 18% of the total individuals greater than 5 cm dbh (Kalacskas et al. 2004). Although *G. ulmifolia* has no timber value, it provides food and shade for cattle and attracts birds and bats into the open pasture, thereby increasing seed dispersal in localities otherwise undesirable for seed dispersers. A higher density of tree species other than *G. ulmifolia* (e.g., *Anacardium excelsum*, *Enterolobium cyclocarpum*, *Andira inermis*) were found regenerating beneath isolated *G. ulmifolia* trees than in surrounding pasture, indicating that this species may function in this

Table 2. A three-way analysis of variance was employed to test the effect of herbicide application, cattle exclusion, and riparian zone on basal area, density, and species number of natural regeneration greater than 1 m in height in experimental plots.

	Basal Area (m^2)	Stem Density	Species Richness
Herbicide			
F	18.79	19.84	9.53
p	<0.0001	<0.0001	0.003
Cattle			
F	20.33	31.74	9.33
p	<0.0001	<0.0001	0.003
Riparian zone			
F	10.82	18.7	23.9
p	0.001	<0.0001	<0.0001

F and p values are given. Data were square root transformed. No interactions were significant. Degrees of freedom equaled 1 for all factors.

Table 3. Indicator species for each factor defined as species where 90% of the stems were associated with a particular treatment in experimental plots within an active pasture in Panama.

Indicator Species	Habit	Regeneration Mode	Dispersal Mode	Preference
Forested riparian				
<i>Annona purpurea</i>	T	C	M, Ba	+
<i>Astronium graveolens</i>	T	S	W	+
<i>Calycophyllum candissimum</i>	T	S/C	W	+
<i>Cecropia peltata</i>	T	S	Ba, Bi	+
<i>Cochlospermum vitifolium</i>	T	C	W	+
Topography				
<i>Chromelia spinulosa</i>	S	S/C	Bi	+
<i>Trema micrantha</i>	ST	S	W	+
<i>C. peltata</i>	T	S	Ba, Bi	–
Cattle				
<i>Co. vitifolium</i>	T	C	W	–
<i>T. micrantha</i>	ST	S	W	–
Herbicide				
<i>A. purpurea</i>	T	C	M, Ba	–
<i>Co. vitifolium</i>	T	C	W	–
<i>T. micrantha</i>	ST	S	W	+

Codes: Habit (ST, small tree; T, tree; S, shrub); regeneration mode (C, coppice; S, seed; S/C, seed & coppice); dispersal mode (Ba, bat; Bi, bird; Ca, cattle; M, mammal; Ro, rodent; W, wind; U, unknown); and preference (+, presence of the factor; –, absence of factor).

system as a nurse tree creating zones of tree initiation for forest succession (Griscom 2004).

As we predicted, cattle had a more negative than positive effect on natural regeneration. Cattle increased light during the wet season, by foraging on grass species and many nongrass species, as was found by other studies (Rummell 1951; Janzen 1988; Karl & Doescher 1993; Belsky & Blumenthal 1997; Posada et al. 2000). At less than 1 head/ha, this positive effect did not balance out their negative effect on natural regeneration. Surprisingly, cattle did not decrease surficial soil moisture (via soil compaction); however, we did not measure moisture below 10 cm, and soil moisture patterns may differ at deeper horizons. For this system, cattle should be excluded from regenerating pastures to maximize woody plant regeneration. This conclusion from our results is paralleled by studies in wet tropical systems (Guevara et al. 1986; Guevara & Laborde 1993; Williams-Linera et al. 1998; Harvey & Haber 1999).

We predicted that herbicide would increase the success of natural regeneration by removing competition with the exotic grasses, *Hyparrhenia rufa* and *Panicum maximum*. Previous studies have shown that exotic grass is a major barrier to forest succession (Buschbacher 1986; Nepstad et al. 1991, 1996; Guariguata et al. 1994; Gerhardt & Fredriksson 1995; Parrotta 1995; Sun & Dickinson 1996; Holl 1998). In another study at this same site, we found that planted seedlings performed best where herbicide had

been applied (Griscom et al. 2005). However, a positive response to herbicide did not occur for natural tree regeneration in terms of stem count and basal area. We suspect that this result is due in part to the importance of root sprouting as a regeneration strategy, a form of regeneration that was eliminated by the herbicide treatment. Herbicide application reduced the density of regenerating stems of trees, shrubs, vines, and herbs. Species that were noticeably absent in herbicided plots were *Annona purpurea*, *Cochlospermum vitifolium*, and *Heliconia lathispata*. The root systems of these species were killed in the herbicide treatment at the beginning of the experiment.

On the other hand, herbicide application significantly increased light levels, which may be a limiting factor for species regenerating from seed in the wet season when tallgrass creates a dense canopy. For example, *Trema micrantha*, a fast-growing, light-demanding species that does not appear to root sprout, regenerated exclusively in the herbicided plots. Herbicide application is recommended only if the species of interest depend upon regeneration from seed. Furthermore, in order to avoid soil erosion and species loss, this treatment should be avoided, particularly in landscapes such as this one with seasonally heavy rainfall and sloped landscapes. We did not detect significant treatment interactions; however, further targeted investigations may uncover interactions. For example, higher replication may detect positive interactions between herbicide, cattle, and deforested riparian zones which when combined generated the lowest plant density and growth rates in this study. We suspect that combining such conditions may pass system thresholds that result in critical soil erosion problems.

Plots associated with forested riparian zones had significantly greater species richness, basal area, and stem density than plots adjacent to deforested riparian zones. Plots associated with forested riparian zones also had substantially higher Shannon diversity and evenness. A few tree species were only found in plots adjacent to riparian zones (e.g., *Astronium graveolens*, *Calycophyllum candissimum*, *Cecropia peltata*). Many frugivorous birds and bats visit riparian zones and may disperse seeds of *C. peltata* into the adjacent open pasture (Griscom et al. 2007). Wind-dispersed seeds from trees within the riparian zones such as *Ca. candissimum* and *As. graveolens* could be mostly restricted to short-distance dispersal into adjacent open pasture localities. The diversity and abundance of flora and fauna in the riparian zones at this study site increased the potential of tree regeneration, mostly of small-seeded species into open pasture sites.

The persistence of coppicing and presence of forested riparian zones suggest that our study area is able to regenerate relatively diverse second-growth forests after pasture abandonment. However, areas isolated from riparian zones can be expected to have a slower successional rate as expressed by lower species richness, stem count, and basal area in our plots. These sites will need to be enrichment planted to increase species diversity and to

accelerate forest succession. Management applications should be site specific and take into account the presence or absence of forested riparian zones.

This study examined the initial 3 years of tree regeneration in one landscape, and questions remain to be addressed regarding the enhancement of forest integrity on the Azuero Peninsula. The next steps in experimental research on native forest regeneration should include investigations on (1) impacts of fire, (2) other landscape types in the Azuero Peninsula region, (3) successional patterns after 3 years since abandonment, and (4) interactions between factors that may result in threshold changes in system response such as soil erosion.

Implications for Practice

- Exclude cattle, apply herbicide, and enrichment plant on flat or gently sloped sites that have little potential to regenerate on their own (areas that are not near forested riparian zones).
- Exclude cattle and do not apply herbicide in sites that do not need to be enrichment planted, are relatively diverse, and have a prevalence of coppicing.
- Based on studies in other neotropical dry forests (Janzen 2002) and observations in our study area, exclusion of fire is as important if not more important than exclusion of cattle for successful forest regeneration.
- If appropriate, reintroduce missing plant species (e.g., *Pachira quinata* (Jacq.) W.S. Alverson, *Dalbergia retusa* Hemsl, *Manilkara zapota* (L.) Van Royen, *Ceiba pentandra* (L.) Gaertn., *Albizia guachapele* (Kunth) Dugand).
- Actively protect forested riparian zones from cattle grazing and fire because they represent the natural regeneration capital of the landscape.

Acknowledgments

We would like to thank The Achotines Laboratory of the International Tropical Tuna Commission and Manager V. Scholey for the use of their research and lodging facilities and Oswaldo and P. Batista for permission to conduct experimental research on their land. Logistical support was provided by Panama Native Species Reforestation Project (PRORENA), a joint program between Smithsonian Tropical Research Institute and the Yale School of Forestry and Environmental Studies. We would especially like to thank M. Wishnie, executive director of PRORENA, for support and advice during this study. The research would not have been possible without the technical support of field assistants, D. Mancilla, R. Mancilla, A. Vergara, D. Vergara, and G. Solis. We would also like to thank J. Deago for his advice on improving the design of this study. Financial support was provided to H. P. Gris-

com by the United States Department of Agriculture fellowship through the Yale School of Forestry and Environmental Studies and The New York Botanical Garden, the graduate fellowship through the Yale Graduate School of Arts and Science, and Yale departments of International Area Studies and Ecology and Evolutionary Biology.

LITERATURE CITED

- Aide, T. M., and J. Cavelier. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* **2**:219–229.
- Aide, T. M., J. K. Zimmerman, J. B. Pascarella, L. Rivera, and H. Marciano-Vega. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology* **8**:328–338.
- Ashton, P. M. S., S. Gamage, I. A. U. N. Gunatilleke, and C. V. S. Gunatilleke. 1997. Restoration of a Sri Lankan rain forest: using Caribbean pine *Pinus caribaea* as a nurse for establishing late successional tree species. *Journal of Applied Ecology* **34**:915–925.
- Ashton, P. M. S., C. V. S. Gunatilleke, B. M. P. Singhakumara, and I. A. U. N. Gunatilleke. 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. *Forest Ecology and Management* **154**:409–430.
- Belsky, A. J., and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conservation Biology* **11**:315–327.
- Bennington, C. C., and W. V. Thyne. 1994. Use and misuse of mixed model analysis of variance in ecological studies. *Ecology* **75**:717–722.
- Bullock, S. H. 1995. Plant reproduction in neotropical dry forests. Pages 277–303 in S. H. Bullock, H. A. Mooney, and E. Medina, editors. *Seasonally dry tropical forests*. Cambridge University Press, New York.
- Buschbacher, R. 1986. Tropical deforestation and pasture development. *BioScience* **36**:22–28.
- Ewel, J. J. 1977. Differences between wet and dry successional tropical ecosystems. *Geo-Eco-Trop* **1**:103–117.
- Ewel, J. J. 1980. Tropical succession: manifold routes to maturity. *Biotropica* **12**:2–7.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* **8**:629–644.
- Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phonological studies of trees in tropical wet and dry forests in lowlands of Costa Rica. *Journal of Ecology* **62**:881–919.
- Gerhardt, K. 1993. Tree seedling development in tropical dry abandoned pasture and secondary forest in Costa Rica. *Journal of Vegetation Science* **4**:95–102.
- Gerhardt, K., and D. Fredriksson. 1995. Biomass allocation by broad-leaf mahogany seedlings, *Swietenia macrophylla* (King), in abandoned pasture and secondary dry forest in Guanacaste, Costa Rica. *Biotropica* **27**:174–182.
- Gerhardt, K., and H. Hytteborn. 1992. Natural dynamics and regeneration methods in tropical dry forests. *Journal of Vegetation Science* **3**:361–364.
- Gillespie, T. W. 1999. Life history characteristics and rarity of woody plants in tropical dry forest fragments of Central America. *Journal of Tropical Ecology* **15**:637–649.
- Griscom, H. P. 2004. Rehabilitation of a dry tropical forest ecosystem in a cattle pasture matrix on the Azuero Peninsula, Panama. Ph.D. dissertation. Yale School of Forestry and Environmental Studies, New Haven, Connecticut.

- Griscom, H. P., M. S. Ashton, and G. P. Berlyn. 2005. Seedling survival and growth of native tree species in pastures: implications for dry tropical forest rehabilitation in central Panama. *Forest Ecology and Management* **206**:45–56.
- Griscom, H. P., E. K. V. Kalko, and P. M. S. Ashton. 2007. Frugivory by small vertebrates within a deforested, dry tropical region of Central America. *Biotropica* **39**:278–282.
- Guariguata, M., R. Rheingans, and F. Montagnini. 1994. Early woody invasion under tree plantations in Costa Rica: implications for forest restoration. *Society for Economic Restoration* **3**:222–260.
- Guevara, S., and L. Laborde. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. *Vegetatio* **107/108**:319–338.
- Guevara, S., J. Meave, P. Moreno-Casasola, and J. Laborde. 1992. Floristic composition and structure of vegetation under isolated trees in neotropical pastures. *Journal of Vegetation Science* **3**:655–664.
- Guevara, S., S. Purata, and E. Van der Maarel. 1986. The role of remnant forest trees in tropical secondary succession. *Vegetatio* **66**:77–84.
- Harvey, C. A., and W. A. Haber. 1999. Remnant trees and the conservation of biodiversity in Costa Rican pastures. *Agroforestry Systems* **44**:37–68.
- Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.
- Holl, K. D. 1998. Effects of above and below ground competition of shrubs and grass on *Calophyllum brasiliense* seedling growth in abandoned tropical pasture. *Forest Ecology and Management* **109**:187–195.
- Holl, K. D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica* **31**:229–242.
- Instituto Geográfico Nacional Tommy Guardia. 1988. Atlas nacional de la República de Panamá/Instituto Geográfico “Tommy Guardia.” 3a ed. El Instituto, Panamá.
- Janzen, D. 1982a. Natural history of Guacimo fruits (*Sterculiaceae: Guazuma ulmifolia*) with respect to consumption by large mammals. *American Journal of Botany* **69**:1240–1250.
- Janzen, D. 1982b. Removal of seeds from horse dung by tropical rodents: influence of habitat and amount of dung. *Ecology* **63**:1887–1900.
- Janzen, D. 1986. Tropical dry forests: the most endangered major tropical ecosystem. Pages 130–137 in E. O. Wilson, editor. *Biodiversity*. National Academy Press, Washington, D.C.
- Janzen, D. 1988. Management of habitat fragments in a tropical dry forest: growth. *Annals of the Missouri Botanical Garden* **75**:105–116.
- Janzen, D. 2002. Tropical dry forest: area de conservación Guanacaste, northwestern Costa Rica. Pages 559–583 in M. Perrow and A. J. Davy, editors. *Handbook of ecological restoration*, vol. II. Cambridge University Press, Cambridge, United Kingdom.
- Kalacska, M., G. A. Sanchez-Azofeifa, J. C. Calvo-Alvarado, M. Quesada, B. Rivard, and D. H. Janzen. 2004. Species composition, similarity, and diversity in three successional stages of a seasonally dry tropical forest. *Forest Ecology and Management* **200**:227–247.
- Karl, M. G., and P. S. Doescher. 1993. Regulating competition on conifer plantations with pre-regulating competition on conifer plantations with prescribed cattle grazing. *Forest Science* **39**:405–418.
- Kennard, D. 2002. Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. *Journal of Tropical Ecology* **18**:53–66.
- Knoop, W. T., and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savannah. *Journal of Ecology* **73**:235–253.
- Maass, J. D. 1995. Conversion of tropical dry forest to pasture and agriculture. Seasonally dry tropical forests. Pages 399–418 in S. H. Bullock, H. A. Mooney, and E. Medina, editors. *Seasonally dry tropical forests*. Cambridge University Press, New York.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey.
- McLaren, K. P., and M. A. McDonald. 2003. Coppice regrowth in a disturbed tropical dry limestone forest in Jamaica. *Forest Ecology and Management* **180**:99–111.
- Mooney, H. A., S. H. Bullock, and E. Medino. 1995. Introduction. Pages 1–9 in S. H. Bullock, H. A. Mooney, and E. Medina, editors. *Seasonally dry tropical forests*. Cambridge University Press, New York.
- Murphy, P. G., and A. E. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* **17**:67–88.
- Murphy, P. G., and A. E. Lugo. 1995. Dry forests of Central America and the Caribbean. Pages 9–34 in S. H. Bullock, H. A. Mooney, and E. Medina, editors. *Seasonally dry tropical forests*. Cambridge University Press, New York.
- Nepstad, D., C. Uhl, C. A. Pereira, and J. M. da Silva. 1996. A comparative study on tree establishment in abandoned pasture and mature forest in eastern Amazonia. *Oikos* **76**:25–39.
- Nepstad, D., C. Uhl, and E. Serrao. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Para, Brazil. Pages 215–229 in A. B. Anderson, editor. *Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest*. Columbia University Press, New York.
- Nepstad, D., C. Uhl, and E. Serrao. 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. *Ambio* **20**:248–255.
- Parrotta, J. 1995. Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. *Journal of Vegetation Science* **6**:627–636.
- Posada, J. M., T. M. Aide, and C. V. Mitchell. 2000. Cattle and weedy shrubs as restoration tools of tropical montane rainforest. *Restoration Ecology* **8**:370–379.
- Rummell, R. S. 1951. Some effects of livestock grazing on Ponderosa pine forest and range in Central Washington. *Ecology* **32**:594–607.
- Russell-Smith, J. 1996. Regeneration of monsoon rain forest in northern Australia: the sapling bank. *Journal of Vegetation Science* **7**:889–900.
- Sabogal, C. 1992. Regeneration of tropical dry forests in Central America, with examples from Nicaragua. *Journal of Vegetation Science* **3**:407–417.
- Sanchez-Azofeifa, G. A., M. Kalacska, M. Quesada, J. C. Calvo-Alvarado, J. M. Nassar, and J. P. Rodriguez. 2005. Need for integrated research for a sustainable future in tropical dry forests. *Conservation Biology* **19**:285–286.
- Scatena, F. N., and A. E. Lugo. 1995. Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steep land and watersheds of Puerto Rico. *Geomorphology* **13**:199–213.
- Searle, S. R., G. Casella, and C. E. McCulloch. 1992. *Variance components*. John Wiley & Sons, New York.
- Sun, D., and G. R. Dickinson. 1996. The competition effect of *Bracharia decumbens* on the early growth of direct-seeded trees of *Alphitonia petriei* in tropical north Australia. *Biotropica* **28**:272–276.
- Swaine, M. D. 1992. Characteristics of dry forest in West Africa and the influence of fire. *Journal of Vegetation Science* **3**:365–374.
- Tomohiro, S., M. S. Ashton, B. Singhakumara, H. P. Griscom, S. Ediriweera, and B. W. Griscom. 2006. Effects of fire on the recruitment of rain forest vegetation beneath *Pinus caribaea* plantations, Sri Lanka. *Forest Ecology and Management* **226**:357–363.
- Vieira, D. L. M., and A. Scariot. 2006. Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology* **14**:11–20.
- Williams-Linera, G., V. Dominguez-Gastelu, and M. E. Garcia-Zurita. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conservation Biology* **12**:1091–1102.

Appendix. Inventoried species by dominance (percentage of total stems) that were encountered more than once in experimental plots in an active pasture in Panama.

Species Name	Family	Habit	Regeneration Mode	Dispersal Mode	Density (Stems/ha)	Basal Area (m ² /ha)
<i>Guazuma ulmifolia</i> Lam.	Sterculiaceae	T	S/C	Ca, Ba	365	0.4939
<i>Clibadium</i> sp.	Compositae	S	S/C	W	124	0.0638
<i>Bauhinia</i> sp.	Leguminosae	S	S/C	W	90	0.0579
<i>Sida</i> sp. (1)	Malvaceae	H	S	W	63	0.0012
<i>Scrophulaceae</i>	Scrophulaceae	H	S	W	58	0.0012
<i>Vernonia</i> sp.	Compositae	S	S/C	W	54	0.0603
<i>Cordia alliodora</i> Ruiz & Pav. (Oken)	Boraginaceae	T	S/C	W	39	0.0342
<i>Casearia arguta</i> Kunth	Flacardiaceae	S	C	Bi	35	0.0016
<i>Machaerium microphyllum</i> (E. Mey.) Standl.	Leguminosae	V	S/C	W	34	0.0182
<i>Hibiscus</i> sp.	Malvaceae	H	S	W	34	0.0030
<i>Bauhinia unguolata</i> L.	Leguminosae	V	S/C	W	33	0.0007
<i>Tabebuia ochracea</i> (Cham) Standl.	Bignoniaceae	T	C	W	31	0.0149
<i>Trema micrantha</i> (L.) Blume	Compositae	ST	S	W	31	0.0675
<i>Chomelia spinosa</i> Jacq.	Rubiaceae	S	S/C	Bi	30	0.0111
<i>Astronium graveolens</i> Jacq.	Anacardiaceae	T	S	W	24	0.0116
<i>Heliconia lathispatha</i> Benth.	Musaceae	H	C	Bi	21	0.0004
<i>Cecropia peltata</i> L.	Cecropiaceae	T	S	Ba, Bi	20	0.0563
<i>Acacia collinsii</i> Saff	Leguminosae	ST	S	Ba	20	0.0174
<i>Annona purpurea</i> (Moc. & Sesse) Dunal	Annonaceae	T	C	M, Ba	18	0.0248
<i>Cochlospermum vitifolium</i> (Willd.) Spreng	Cochlospermaceae	T	C	W	17	0.0273
<i>Stigmaphyllon</i> sp.	Malphigaceae	V	S	Bi	16	0.0003
<i>Coccoloba coronata</i> Jacq.	Polygonaceae	T	C	Bi	15	0.0130
<i>Cordia</i> sp.	Boraginaceae	T	C	Bi	14	0.0103
<i>Calycophyllum candissimum</i> (Vahl) DC	Rubiaceae	T	S/C	W	14	0.0048
<i>Aphelandra sinclairiana</i> Nees	Acanthaceae	H	S/C	W	12	0.0002
<i>Stemmadenia grandiflora</i> (Jacq.) Miers	Apocynaceae	S	C	Bi	12	0.0033
<i>Malphigia</i> sp.	Malphigaceae	S	S/C	Bi	12	0.0024
<i>Hura crepitans</i> L.	Euphorbiaceae	T	S	E	11	0.0126
<i>Eugenia coloradensis</i> Standl.	Myrtaceae	T	C	Bi, Ba, M	10	0.0053
<i>Diphysa robinoides</i> Benth	Leguminosae	T	C	E	9	0.0052
<i>Lonchocarpus velutinus</i> Benth	Leguminosae	T	S/C	W	9	0.0013
<i>Piper marginatum</i> Jacq.	Piperaceae	H	S	Ba	9	0.0002
<i>Ta. rosea</i> (Bertol). DC	Bignoniaceae	T	S	W	8	0.0064
<i>Bursera simaruba</i> (L.) Sarq	Burseraceae	T	S	Bi	8	0.0085
<i>Combretum fruticosum</i> (Loefl) Stuntz	Combretaceae	S	C	W	8	0.0040
<i>Cor. panamensis</i> L. (Riley)	Boraginaceae	T	C	Bi	7	0.0060
<i>Muntingia calabura</i> L.	Eleoocarpaceae	ST	S	Bi/Ba	7	0.0121
<i>Genipa americana</i> L.	Rubiaceae	T	S	M, Bi	7	0.0013
<i>Tournefortia cuspidate</i> Kunth	Boraginaceae	V	S	Bi	6	0.0001
<i>Albizia adenocephala</i> (J.D. Sm.) Birtt. & Rose	Leguminosae	T	S	W	5	0.0033
<i>Triumfetta lappula</i> L.	Tiliaceae	H	S	W	5	0.0001
<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.	Leguminosae	T	S	Ca, Ro	4	0.0021
<i>Psidium guajava</i> L.	Myrtaceae	S	C	Bi, Ba	4	0.0017
<i>Pithecellobium hymenaeifolium</i> (Willd.) Benth	Leguminosae	V	U	Bi	3	0.0001
<i>Thevetia ahouai</i> (L.) A.DC.	Apocynaceae	S	S	Bi	2	0.0002
<i>Sida</i> sp. (2)	Malvaceae	H	S	W	2	0.0001
<i>Chlorophora tinctoria</i> (L.) Gaud.	Moraceae	T	C	Ba	2	0.0047
<i>Pouteria campechiana</i> (Kunth) Baehni	Sapotaceae	ST	C	Ba, Bi, M	2	0.0976
<i>Luehea speciosa</i> Willd.	Tiliaceae	T	C	W	2	0.0141
<i>Spondias mombin</i> L.	Anacardiaceae	T	S	Ca, Ba, Bi	2	0.0017
<i>Sciadodendron excelsum</i> Griseb.	Araliaceae	T	C	Bi	2	0.0012
<i>Hymenaea courbaril</i> L.	Leguminosae	T	C	M	2	0.0017
<i>Sapium glandulosum</i> (L.) Morong	Euphorbiaceae	T	S	Bi	1	0.0015

Codes: Habit (H, herb; V, vine; ST, small tree; T, tree); regeneration mode (C, coppice; S, seed; S/C, seed & coppice; U, unknown); and dispersal mode (Ba, bat; Bi, bird; Ca, cattle; M, mammal; Ro, rodent; W, wind).

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