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

Heather P. Griscom,[1,2] Bronson W. Griscom,[1] and Mark S. Ashton[1]

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 ecosystems (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,

[1] PRORENA Program, School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, U.S.A.
[2] Address correspondence to H. P. Griscom, email hgriscom@aya.yale.edu

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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., *Guazuma* spp.) (Janzen 1982*a*, 1982*b*, 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 second 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 Cretacean 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

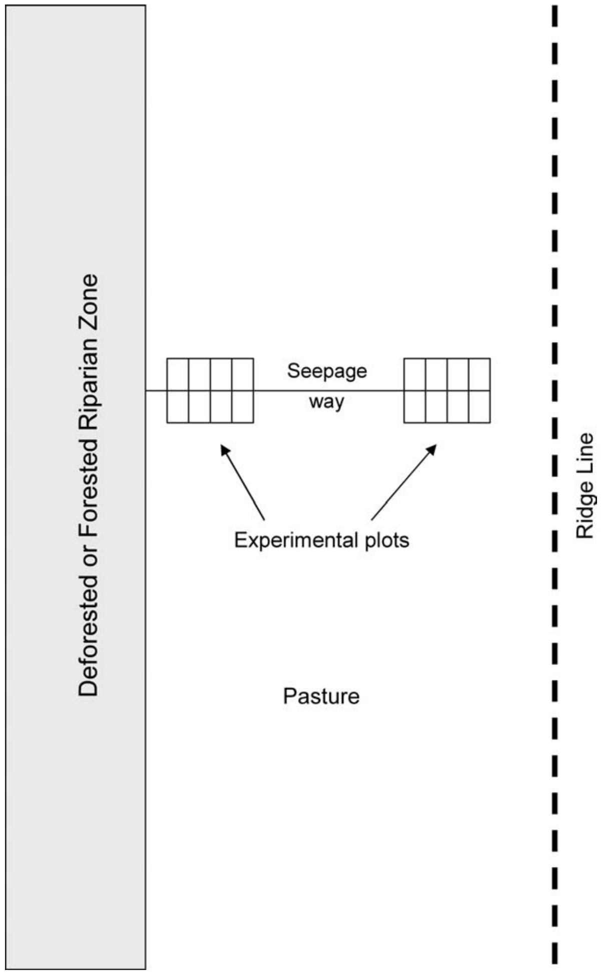

Figure 1. Landscape layout of the experimental plots. Plots (9 × 12 m) were located along seepage ways adjacent to forested or deforested riparian zones. Eight plots were located in a "downslope," and eight plots were located in an "upslope" set.

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 application 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

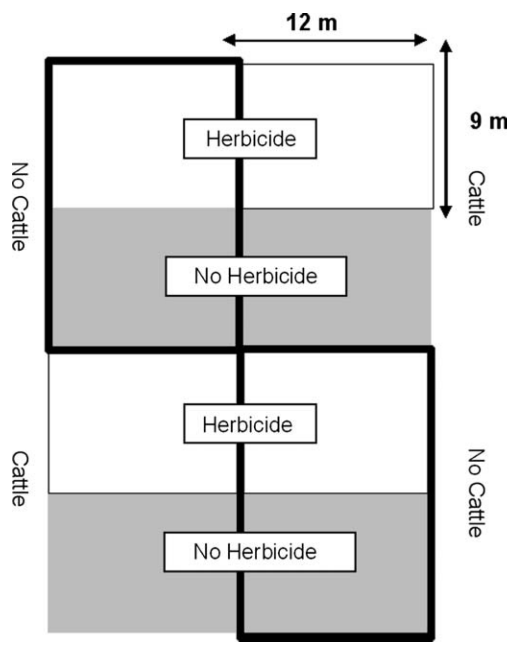

Figure 2. Design of experimental plots (8 of 16 plots shown). This model was replicated six times (three adjacent to forested riparian zones and three adjacent to deforested riparian zones) within an 85-ha pasture in Panama.

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-m^2 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 m^2) 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)
F	22.5	0.01	26.4	12.61	19.7	31.59
p	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)
F	12.2	0.85	3.1	0.3	28.8	0.21
p	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)
F	89.6	5.13	0.05	4.29	1.61	0.89
p	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 m^2/100 m^2) and stem density (19 stems/100 m^2) compared to plots with cattle, which had an average basal area of 0.013 m^2/100 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).

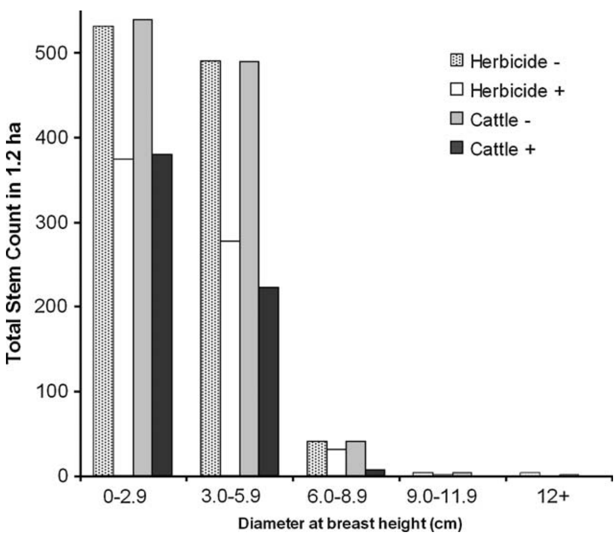

Figure 3. Total stem count of natural regeneration by dbh (cm) after 3 years in experimental plots. All plots in each treatment were pooled together. Factors: cattle and herbicide; (+), presence of the factor; (−), absence of factor.

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 m^2/100 m^2) than non-herbicided plots, which had a stem density of 18 stems/100 m^2 and basal area of 0.026 m^2/100 m^2. The largest stems were found in non-herbicided 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-herbicided 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 herbicided plots; $H = 3.00$, $E_H = 0.70$ in non-herbicided 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 m^2/100 m^2 vs. 0.015 m^2/100 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 herbicided

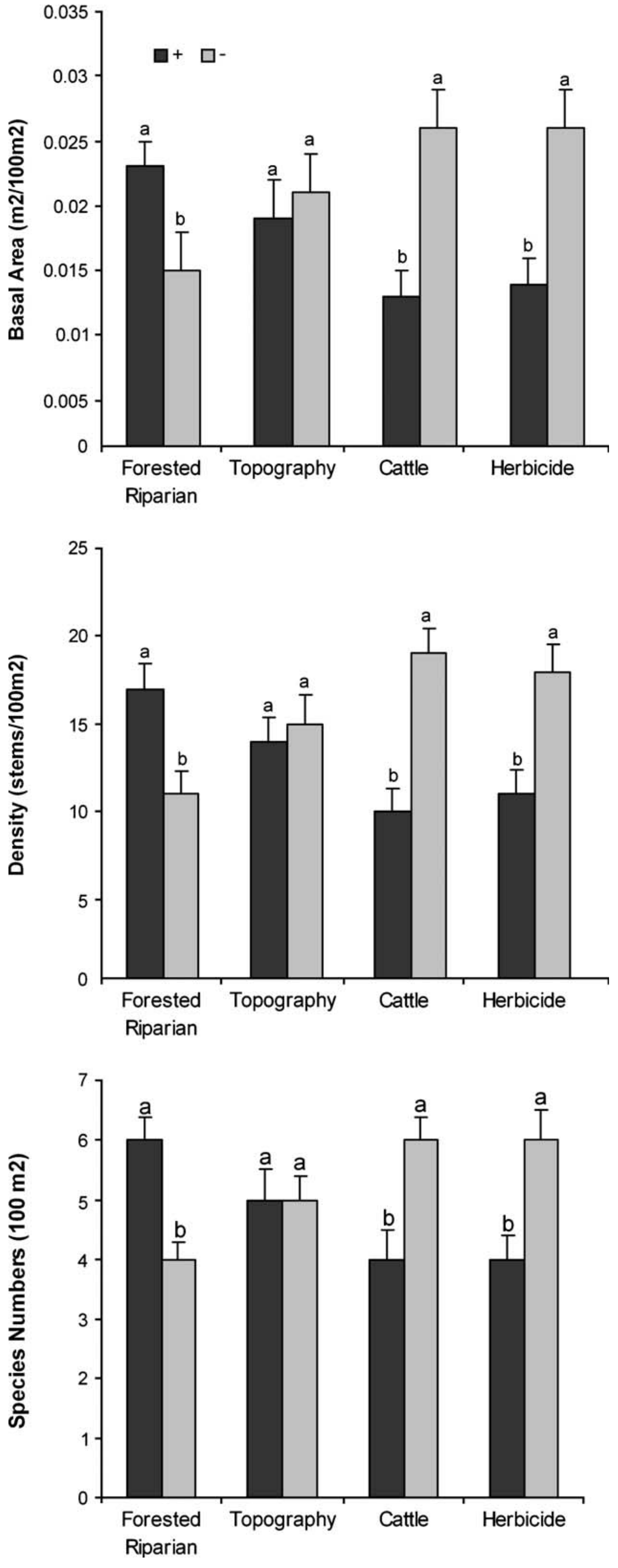

Figure 4. Mean basal area (m^2/100 m^2), density (stems/100 m^2), and species number (100 m^2) of natural regeneration greater than 1 m in height in experimental plots. (+), presence of the factor; (−), absence of factor. Topography (+), upper slope; (−), lower slope. Significance ($p < 0.05$) are assigned 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 (Kalacska 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				
Annona purpurea	T	C	M, Ba	+
Astronium graveolens	T	S	W	+
Calycophyllum candissimum	T	S/C	W	+
Cecropia peltata	T	S	Ba, Bi	+
Cochlospermum vitifolium	T	C	W	+
Topography				
Chromelia spinulosa	*S*	S/C	Bi	+
Trema micrantha	ST	S	W	+
C. peltata	T	S	Ba, Bi	−
Cattle				
Co. vitifolium	T	C	W	−
T. micrantha	ST	S	W	−
Herbicide				
A. purpurea	T	C	M, Ba	−
Co. vitifolium	T	C	W	−
T. micrantha	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 lathispatha*. 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.

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