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Seedling survival and growth of native tree species in pastures: Implications for dry tropical forest rehabilitation in central Panama

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Abstract

Our study tested the effects of herbicide application and cattle removal on the survival and growth of three native tree species planted in pastures within a deforested, dry tropical region of Panama. We investigated whether enrichment planting may be a potential, complementing reforestation tool with natural regeneration. Three economically valuable tree species were chosen for the study; *Cedrela odorata* L., *Enterolobium cyclocarpum* (Jacq.) Griseb, and *Copaifera aromatica* Dwyer. Planted seedlings were monitored for survival, root collar diameter and height growth in the presence or absence of two factors; (1) initial herbicide application and (2) cattle. After 16 months, subsamples of seedlings within each treatment were harvested and measured for dry masses and leaf areas. In the initial stages of development, *C. odorata* seedlings had the greatest growth rates with herbicide application whereas *E. cyclocarpum* seedlings had the greatest growth rates with cattle exclusion. The combination of these two factors yielded the best growth for both species. Of the three species, *C. odorata* had the lowest mortality rates (58%), and the greatest average dry mass (μ = 403.7 g), leaf area (μ = 169.3 m^2), diameter growth rate (μ = 3.7 cm year^{-1}) and height growth rate (μ = 81.7 cm year^{-1}) at 16 months. In addition, in the presence of cattle, *C. odorata* grew significantly better than *E. cyclocarpum*. To accelerate forest succession, herbicide should be applied initially and cattle removed before enrichment planting.

Keywords: Cattle; *Cedrela odorata*; *Copaifera aromatica*; Enrichment planting; *Enterolobium cyclocarpum*; Herbicide; Panama; Pastures; Rehabilitation; Tropical dry forest

1. Introduction

Dry tropical forests were the most common forest type along the Pacific coast of Central America until conversion to pasture for cattle ranching reduced the

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forested landscape into a fraction of its original size (Janzen, 1986a). The trend began in the early part of the 20th century and reached its peak in the 1960's and 1970's (Janzen, 1983). In Central America, pastures have remained productive for decades (Reiners et al., 1994; Aide et al., 1996; Thomlinson et al., 1996; Harvey and Haber, 1999; Holl, 1999). However, in the foothills on the Pacific side of Western Panama, yearly pasture burning and heavy rainfall during the wet season have caused severe erosion and a steady decline in land productivity (Heckadon-Moreno, 1984). Degraded pastures may follow several pathways: (1) the land may remain a subsistence pasture in a permanent state of arrested forest succession if fire disturbance continues; (2) larger cattle owners may buy the land and invest in superior ranching techniques; (3) investors may convert the land to teak plantations or; (4) land owners and conservation agencies may wish to rehabilitate the land into a native forest that supports a diversity of plant and animals species and that provides ecosystem services, such as carbon sequestration and soil and water conservation. This paper examines the potential of the latter trajectory.

Reforestation with native species may be the most cost-effective and realistic strategy for rehabilitating pastures to one with productive uses, whereby the regeneration potential of existing vegetation is exploited with limited human manipulation (Lugo, 1988). Other more intensive strategies, such as reforestation with exotic or native nurse tree plantation systems, although highly effective (Parrotta, 1992; Guariguata et al., 1994; Ashton et al., 1997; Montagnini, 2001) are more costly and time-intensive. As an alterative, natural forest succession may be accelerated and enhanced through limited planting and tending. Enrichment planting can effectively introduce functional groups that may otherwise be missing. For example, large-seeded species are often unable to colonize open pastures due to lack of animal seed-dispersers and/or heavy seed-predation (Janzen, 1986b, 1988; Nepstad et al., 1990; Parotta et al., 1997). However, for both natural regeneration and enrichment planting, success may be dependent on site treatments that modify harsh, environmental conditions within pasture environments.

Grazing protection may be a positive intervention strategy. Cattle can cause detrimental changes to soil properties by compacting the soil, thereby increasing soil water run-off and decreasing the availability of water and nutrients (Fleischner, 1994; Belsky and Blumenthal, 1997). Cattle may also negatively affect seedling growth rate and survival by trampling and browsing on seedlings (Guevara et al., 1986; Guevara and Laborde, 1993; Williams-Linera et al., 1998; Harvey and Haber, 1999). However, animals may have a positive effect on seedling growth by decreasing grass biomass, thereby decreasing plant competition for light, water, and nutrients (Janzen, 1988; Karl and Doescher, 1993). Although the effect of cattle on natural regeneration of woody species has been studied in temperate and wet tropical regions (Zimmerman and Neuenschwander, 1984; Belsky and Blumenthal, 1997; Posada et al., 2000), their effect on planted seedlings in pastures within dry tropical forest regions has not been adequately examined. Cattle have been found to decrease resource competition by decreasing grass biomass (Belsky and Blumenthal, 1997; Posada et al., 2000) but they also negatively alter ecosystem processes and decrease species richness and diversity (Posada et al., 2000).

Herbicide application may represent another positive management strategy that may improve seedling growth rates by decreasing plant competition for abiotic resources. In wet tropical systems, the removal of above or below-ground vegetation has been found to increase growth rates of planted seedlings (Nepstad et al., 1990; Holl, 1998; Hooper et al., 2002). However, in a dry tropical system, Gerhardt (1993) found that the effect of vegetation removal on mortality and growth rates of four tree species was species-specific.

Planted seedlings in experimental plots can serve as controlled standards to test the effect of site treatments on plant growth and survival. In this study, seedlings of three, economically valuable, native tree species were used to test the effects of cattle and herbicide on measured variables. We hypothesize that cattle and herbicide application affect growth and survival of planted seedlings. We predict that the removal of grazers and grass cover will improve growth and survival of seedlings during the initial stages of development. The three selected tree species chosen for our study vary in terms of seed size, shade requirements, and dispersal mechanisms and therefore, may be affected differently by experimental treatments.

2. 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 (7°15′30″N, 80°00′15″W), 1–2 km from the coast. Experimental plots were near the Achotines Tuna Laboratory, which received 1300 mm of rainfall in 2002–2003. The dry season is pronounced with 4 months out of the year receiving no rain (December through March). Rain begins in late April and ends in late November.

Basalt is the underlying geology, laid down during the Cretacean era (Instituto Geográfico Nacional Tommy Guardia, 1988). The soils are young and relatively nutrient rich (cation exchange capacity = 21 meq/100 g). Soil textures range from clay loam to clay (Griscom, 2004). In the 1940's–1950, the original dry tropical forest was transformed into pasture for cattle ranching, although a few fragments of secondary forest remained. The undulating terrain, ranges in elevation from 10 to 100 m and now comprises a mosaic of pastures planted with African grasses, *Hyparrhenia rufra* (Jaragua) and *Panicum maximum* (Marisuri), forested riparian zones, isolated trees, and live fences. Experiments were conducted in an 85 ha pasture. The land is currently grazed by a herd of 50–70 Brahman cattle from mid July to mid March (~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. A part of the land is cleared of shrubs and small trees every year. No fire is intentionally used, although accidental fire, burning portions of the pasture, is a yearly phenomenon.

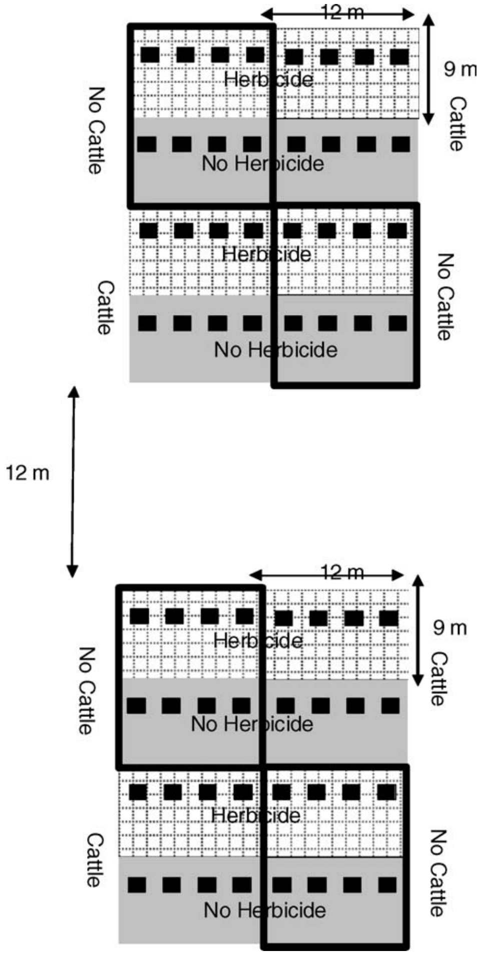

Fig. 1. Experimental design. Sixteen plots (each 12 m × 9 m), separated by 20 m, are shown. This model was replicated nine times within an 85 ha pasture in Panama. The constructed 2^2 factorial experimental design was cattle (+) or no cattle (0) and herbicide application (+) or no herbicide application (0). Black squares represent planted seedlings within experimental plots.

3. Methods and materials

3.1. Experimental design

Initially, a global positioning system was used to map out the dimensions of the 85 ha pasture on a georeferenced photograph. Nine locations, separated by at least 100 m, were randomly selected. At each location, two sets of eight 9 × 12 m plots separated by 20 m were established for a total of 144 plots (Fig. 1). The plots ranged in steepness from 16 to 25°. A 2 × 2 factorial experimental design was constructed: herbicide (+/0); cattle (+/0). Thus, experimental plots were characterized by one of four, randomly assigned treatments: (1) cattle and herbicide application (C_+H_+); (2) cattle and no herbicide application (C_+H_0); (3) cattle exclusion and herbicide application (C_0H_+); (4) cattle exclusion and no herbicide application (C_0H_0).

Plot locations were initially cleared with machetes of pre-existing vegetation (trees, shrubs, vines) at the beginning of the 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. After the cattle fences were constructed, Roundup® herbicide (glyphosate) was applied evenly to designated plots during the early part of the rainy season. Herbicide application was repeated 2 months later during the mid rainy season. Plots were protected from fire in the dry season by constructing fire breaks.

3.2. Planted seedlings

Three native species, *Cedrela odorata* L. (Spanish Cedar, Meliaceae), *Enterolobium cyclocarpum* (Jacq.) Griseb (Ear Tree, Family; Leguminosae, Subfamily; Mimosiodeae), and *Copaifera aromatica* Dwyer (Cabimo, Family; Leguminosae, Subfamily; Papilionoideae) were selected for plantings within the experimental plots based on their different autecologies. *Cedrela odorata* is a small-seeded (0.02 g), wind-dispersed, deciduous, shade-intolerant, canopy timber species that occurs in wet and dry tropical forests of the region (Croat, 1978; Flores, 1998; Navarro et al., 2002; Rocas, 2002). *Enterolobium cyclocarpum* is a medium-seeded (0.75 g), cattle-dispersed, deciduous, shade-intolerant, canopy timber species that occurs in dry tropical forest lowlands on the Pacific side of Central America (Croat, 1978; Janzen, 1983). This species, which provides shade and fodder for cattle, is a common isolated tree in pastures within dry tropical regions (Janzen, 1983). *Copaifera aromatica*, occurring in wet and dry tropical forests, is a medium-seeded (0.70 g), bird and potentially bat-dispersed, evergreen, shade-tolerant, canopy tree that produces timber as well as medicinal resin (Martin and Flores, 2002).

Seeds collected from parent trees for each species were germinated beneath shade-cloth. Two-month-old seedlings of *C. odorata* (μ = 11.5 cm in height) and *C. aromatica* (μ = 7.5 cm in height) and 1-month-old seedlings of *E. cyclocarpum* (μ = 26 cm in height) were out-planted during the rainy season (July 2002). In order to evaluate comparative growth, four seedlings were planted in each experimental plot, one of each species, and one subreplicate of either *C. odorata* or *E. cyclocarpum*. Seedlings were randomly selected and planted 2 m apart. A total of 216 *C. odorata*, 216 *E. cyclocarpum*, and 128 *C. aromatica* seedlings were planted. *Cedrela odorata* and *E. cyclocarpum* initially had 36 replications per treatment. *Copaifera aromatica* had 32 replications per treatment.

Height and root collar diameter (at 5 cm) were measured 2 weeks after seedlings were planted, giving the initial values. Dead seedlings (12 *C. odorata*, two *C. aromatica*, and four *E. cyclocarpum*) were replaced at this time by seedlings of approximately the same size. Seedlings were measured again at 3, 6, 11, 13, and 16 months (July 2002 until November 2003). Growth rates (cm year^{-1}) were calculated after 16 months. Additional growth measurements were made at 28 months (November 2004) for seedlings that were left after destructive sampling.

After 16 months and two growing seasons (November 2003), a random, subsample of *C. odorata* (n = 31), *E. cyclocarpum* (n = 46), and *C. aromatica* (n = 8) seedlings were destructively sampled for measurement of dry mass and leaf area. Specimens were extracted from the soil, roots were washed, fresh weights were obtained, and all samples were air-dried in the field. Samples were then oven dried at 80 °C for 2–10 days. Subsamples of roots, stems, and leaves were weighed each day to create a drying curve. Dry measurements were recorded once samples reached stable weights.

A subsample of three randomly selected leaves per harvested specimen of *C. odorata* were taken for leaf area measurements using the LICOR 3100 area meter (LICOR, Lincoln, NE). Total leaf area was calculated for each *C. odorata* plant by multiplying mean individual leaf and rachis area of the three subsamples by the number of leaves on the plant. For *E. cyclocarpum* and *C. aromatica*, all leaves from each specimen were measured. Leaf area was calculated independently for leaves and rachis.

3.3. Microclimate conditions

3.3.1. Light

Light environment 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.) into exposed sky or sky obscured by plants or slope. 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).

3.3.2. Soil moisture

For 1 year (October 2003–November 2004), soil samples were collected to 10 cm depth every 2 weeks close to a randomly selected seedling in the experimental plots. Relative soil moisture values were determined by recording field wet weight values, drying the samples in the oven at 80 °C for 7 h, and then reweighing the samples. Percent soil moisture contents were calculated from the following equation:

$$\text{soil water content}\,(\%) = ((\text{wet wt}\,(\text{g}) - \text{dry wt}\,(\text{g}))/\text{dry wt}\,(\text{g})) \times 100.$$

3.3.3. Soil nutrients and texture

Soil samples (200 g) were collected from each plot for nutrient and texture analysis. Samples within the same treatment and same site location were combined, by taking an even amount from each sample. Soil samples (100 g) were sent to the University of Georgia Soil, Plant and Water laboratory for nutrient analysis. Extractable nutrients (Ca, K, Mg, Mn, P, and Zn) were analyzed using Malich 1 extraction method (Mehlich, 1953). Percent carbon, nitrogen, and sulfur were analyzed using a Leco CNS 2000 machine (Kirsten, 1979). pH was determined with the wet method (1:1 ratio of water to soil) (Schofield and Taylor, 1955). Texture (sand, silt, clay percent) was analyzed using the hydrometer method at Yale University (Bouyoucos, 1936).

3.3.4. Soil bulk density

To measure bulk density, soil was collected inside the plots, using a 10 cm × 10 cm steel square of 5 cm depth, equaling a volume of 500 cm^3. A piece of wood was laid over the square, which was then hammered into the soil until the square was level with the soil surface, previously cleared of grass and litter. Soil was carefully removed from inside the square with a small trowel and placed in numbered bags. A 10 cm × 5 cm flat piece of metal was inserted inside the square to ensure a level surface at 5 cm depth. Soil was dried for 24 h at 105 °C. Soil volume was calculated as oven dry weight (g)/volume (cm^3).

3.4. Data analysis

Cedrela odorata and *Enterolobium cyclocarpum* data were analyzed using S-Plus software (S-Plus 2000 Professional Release 3, Mathsoft, INC) as an unbalanced, two-way ANOVA where the presence or absence of herbicide application and cattle were the independent variables. The effect on the means of dependent variables were analyzed using the following equation: dependent variable (Y) = cattle (main effect A) × herbicide (main effect B) × interaction (cattle × herbicide) + Type III error. When necessary, data was transformed by log, natural log or arcsine to meet the assumption of homoscedasticity. To normalize

Table 1
Percent of *Cedrela odorata*, *Enterolobium cyclocarpum*, and *Copaifera aromatica* seedling mortality at 16 months caused by cattle, grass loading, insects, rodents, and desiccation within a dry tropical forest region

	C. odorata ($N = 216$) (%)	*E. cyclocarpum* ($N = 216$) (%)	*C. aromatica* ($N = 128$) (%)	Total (%)
Cattle Herbivory	2.8	18.1	0.0	20.8
Cattle Trampling	24.1	19.4	25.0	68.5
Grass Loading	5.1	7.4	0.0	12.5
Insects	9.3	4.6	0.0	13.9
Rodents	0.0	15.7	0.0	15.7
Dessication	0.0	0.0	62.5	62.5
Unknown	16.8	0.0	0.0	16.8
Total Mortality	58.0	65.0	88.0	

Total morality for each species combining all treatments is given.

growth rate data, relative growth rates (cm year^{-1}) were calculated using the following equation: RGR = $(\ln W_2 - \ln W_1)/(t_2 - t_1)$ where W represents either height or root collar diameter at t_1 at the beginning of the experiment and t_2 at the end of the experiment.

χ^2-Statistics were used to analyze mortality data. *Copaifera aromatica* growth rates were not statistically analyzed because the sample size was insufficient.

4. Results

4.1. Seedling mortality

Trampling on the seedlings by cattle was the most common cause of mortality, followed by cattle herbivory, canopy grass loading and insects (Table 1). Death by rodent excavation was unique to *Enterolobium cyclocarpum*. Between 13 and 16 months, dried, gnawed-off stems and missing roots suggested that *Sigmodon hispidus*, a commonly captured rodent within the pasture (Griscom, 2004), had killed *E. cyclocarpum* seedlings.

Hypsipyla grandella, the mahogany shoot-borer, attacked 19% of *Cedrela odorata* seedlings between six and 11 months (39% after 32 months) but this infestation did not result in mortality. Overall, *C. odorata* had lower seedling mortality (58%) than *E. cyclocarpum* (65%) and *Copaifera aromatica* (88%). After 32 months, *C. odorata* still had the lowest mortality rate (5% of the 18 sampled seedlings were dead). On the other hand, 35% of the 26 sampled *E. cyclocarpum* seedlings had died.

Herbicide had a greater significantly positive effect ($\chi = 13.45$, $p < 0.01$) on the survival of *C. odorata*

Table 2
Mean values for yearly height growth rate (HGR) (cm year^{-1}), diameter growth rate (DGR) (cm year^{-1}), total biomass (g) and leaf area (m^2) at 16 months for *Cedrela odorata*, *Enterolobium cyclocarpum*, and *Copaifera aromatica* seedlings within an active pasture in Panama

	C. odorata	*E. cyclocarpum*	*C. aromatica*
HGR (cm year^{-1})	81.7	94.9	21.1
DGR (cm year^{-1})	2.7	1.1	0.3
Leaf number	20	47	10
Leaf area (m^2)	169.33	7.87	6.23
Total biomass (g)	412.5	123.2	16.2
Above-ground biomass (g)	305.2	63.3	13.1
Below-ground biomass (g)	107.3	59.9	3.01
Root mass ratio	0.26	0.49	0.19
Stem mass ratio	0.74	0.51	0.81

Table 3
Effects of herbicide and cattle on yearly growth rate of *Cedrela odorata* and *Enterolobium cyclocarpum* seedlings in an active pasture

	HGR (cm year^{-1})	DGR (cm year^{-1})
C. odorata		
Treatment		
C_+H_+ ($n = 21$)	62.0 (27.8)	2.6 (0.8)
C_+H_0 ($n = 7$)	58.3 (30.5)	1.7 (0.8)
C_0H_+ ($n = 30$)	106.7 (29.6)	3.5 (1.1)
C_0H_0 ($n = 15$)	70.0 (32.0)	1.8 (1.1)
Factor		
Cattle		
F	3.2	0.18
p-Value	ns	ns
Herbicide		
F	11.43	28.54
p-Value	0.001	0.001
Interaction		
F	7.31	1.29
p-Value	0.01	ns
E. cvclocarpum		
Treatment		
C_+H_+ ($n = 17$)	39.4 (17.9)	0.6 (0.1)
C_+H_0 ($n = 4$)[a]	84.7 (59.4)	0.8 (0.4)
C_0H_+ ($n = 22$)	113.9 (14.3)	1.4 (0.4)
C_0H_0 ($n = 14$)	109.2 (29.9)	1.0 (0.3)
Factor		
Cattle		
F	19.76	14.72
p-Value	0.00001	0.001
Herbicide		
F	1.23	0.65
p-Value	ns	ns
Interaction		
F	6.03	2.01
p-Value	0.05	ns

Mean values for height (HGR) and root collar diameter growth rates (DGR) (cm year^{-1}) by treatment are reported. Standard deviations and sample sizes (n) are given in parentheses. *F* values and significance values for two-way analysis of variance of total height and diameter relative growth rates (cm year^{-1}) in field experiments in Panama. C_+H_+: cattle and herbicide application; C_+H_0: cattle and no herbicide application; C_0H_+: cattle exclusion and herbicide application; C_0H_0: cattle exclusion and no herbicide application; ns: not significant

[a] Treatment not included in analysis.

seedlings than cattle exclusion ($\chi = 5.83$, $p < 0.05$). Cattle exclusion had a greater significantly positive effect ($\chi = 7.72$, $p < 0.01$) than herbicide ($\chi = 5.96$, $p < 0.05$) on the survival of *E. cyclocarpum*. The combination of the presence of cattle and absence of herbicide (C_+H_0), resulted in the greatest mortality of *C. odorata* (87% of seedlings) and *E. cyclocarpum* (93% of seedlings). In comparison, only 24% of *C. odorata* seedlings and 19% of *E. cyclocarpum* seedlings died within the cattle exclusion and herbicide application treatment (C_0H_+).

4.2. Growth rates

After 16 months, *Cedrela odorata* had the greatest yearly diameter growth rate (DGR) whereas *Enterolobium cyclocarpum* had the greatest yearly height growth rate (HGR) (Table 2). After 28 months, *C. odorata* had the greatest growth rates for both height and diameter.

ANOVA results showed that herbicide application significantly increased growth rates for *C. odorata* whereas cattle exclusion increased growth rates of *E. cyclocarpum* (Table 3). However, the interaction between the two factors significantly affected relative height growth rates for both species. In the presence of cattle, herbicide application has a negative effect. *Cedrela odorata* growth rates were consistently greatest in the absence of cattle and with herbicide application (Fig. 2a and b). Herbicide application decreased *E. cyclocarpum* height growth but not diameter (Fig. 2c and d). However, despite these differences shown by factor analysis, both species had the greatest growth rates when cattle

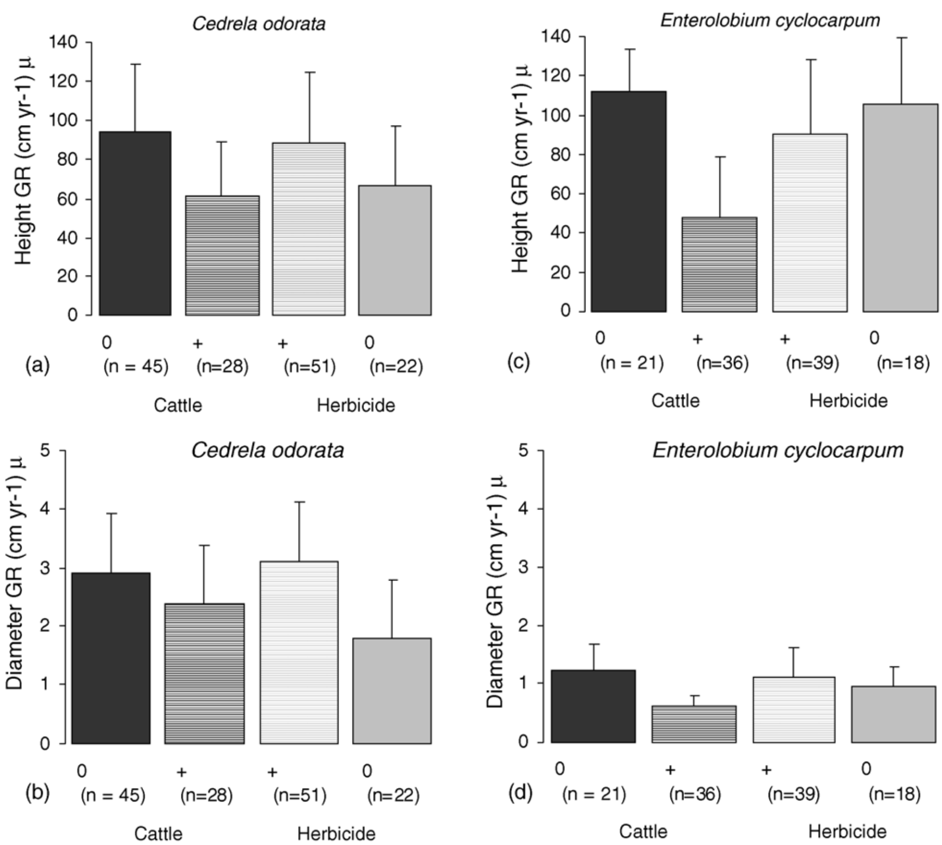

Fig. 2. *Cedrela odorata* and *Enterolobium cyclocarpum* mean height and root collar diameter growth rates (GR) (cm year^{-1}) by factor. Factors: cattle (+) or no cattle (0) and herbicide application (+) or no herbicide application (0). Seedlings were out-planted in experimental treatments within an active, 85 ha cattle pasture in Panama. Bars indicate one standard deviation from the mean. Sample sizes are given in parentheses.

were excluded and herbicide was applied (C_0H_+) (Table 3).

4.3. Destructive sampling: dry mass and leaf area

Cedrela odorata had the greatest biomass and leaf area (Table 2). Unlike growth rates, the presence of cattle significantly decreased *C. odorata* dry mass (Table 4a, Fig. 3a). Conversely, *Enterolobium cyclocarpum* dry mass reflected the same trends as growth rates (Table 4b). Only cattle significantly reduced total dry mass (Fig. 3b). However, the interaction between the two factors was significant, suggesting that in the presence of cattle, herbicide application has a negative effect. As with growth rates, the combination of cattle exclusion and herbicide application (C_0H_+) produced the greatest dry masses of seedlings for both species (Table 4). The combination of

Table 4
Effects of herbicide and cattle on dry mass values of *Cedrela odorata* (a) and *Enterolobium cyclocarpum* (b) seedlings within an active pasture in a dry tropical region

	Total biomass (g)	Below-ground (g)	Above-ground (g)
(a) *C. odorata*			
Treatment			
C_+H_+ ($N = 8$)	183.7 (91.7)	48.2 (16.1)	135.5 (81.0)
C_+H_0 ($N = 7$)	240.3 (369.9)	77.7 (136.7)	162.6 (225.1)
C_0H_+ ($N = 8$)	930.3 (454.8)	236.1 (140.6)	694.3 (337.9)
C_0H_0 ($N = 7$)	274.2 (329.2)	63.5 (77.1)	210.8 (252.9)
Factor			
Cattle			
F	8.6	6.7	9.2
p-Value	0.01	0.05	0.005
Herbicide			
F	8.8	9.6	7.5
p-Value	0.01	0.005	0.01
Interaction			
F	1.5	1.6	1.5
p-Value	ns	ns	ns
(b) *E. cyclocarpum*			
Treatment			
C_+H_+ ($N = 15$)	28.2 (17.6)	15.1 (10.2)	13.1 (8.1)
C_+H_0 ($N = 2$)[a]			
C_0H_+ ($N = 18$)	231.5 (112.1)	114.0 (64.2)	117.5 (61.6)
C_0H_0 ($N = 9$)	100.1 (67.3)	44.9 (33.0)	55.1 (35.0)
Factor			
Cattle			
F	46.7	31.3	51
p-Value	0.00001	0.00001	0.00001
Herbicide			
F	1.1	1.8	0.21
p-Value	ns	ns	ns
Interaction			
F	6.4	3.8	7.7
p-Value	0.01	0.05	0.01

Mean values for above, below and total dry mass (g) at 16 months by treatment are given. Standard deviations and samples sizes (*n*) are in parentheses. *F* values and significance values for two-way analysis of variance of measured variables are given. C_+H_+: cattle and herbicide application; C_+H_0: cattle and no herbicide application; C_0H_+: cattle exclusion and herbicide application; C_0H_0: cattle exclusion and no herbicide application; ns: not significant.

[a] Treatment not included in analysis.

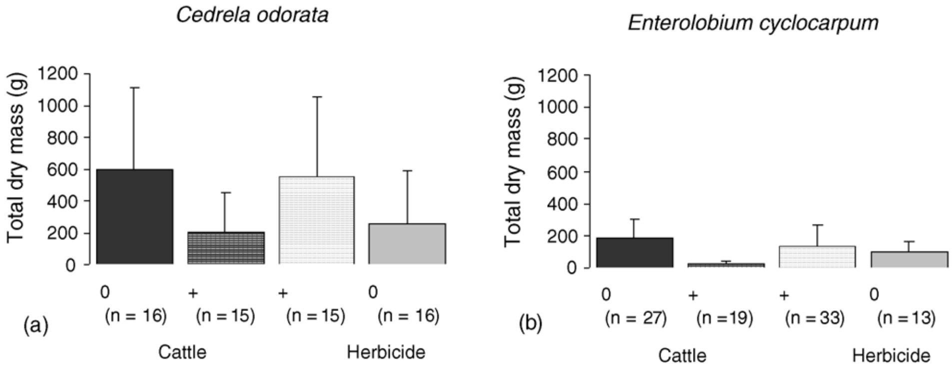

Fig. 3. Effects of herbicide and cattle on mean total dry mass of *Cedrela odorata* and *Enterolobium cyclocarpum* seedlings harvested after 16 months of growth within an active pasture in Panama. Factors: cattle (+) or no cattle (0) and herbicide application (+) or no herbicide application (0). Sample sizes are given in parentheses. Bars indicate one standard deviation from the mean.

cattle and herbicide application (C_+H_+) produced the smallest seedlings for both species.

4.4. Microclimate conditions

During the first wet season (corresponding to the first 5 months of seedling establishment), the presence of cattle and herbicide application significantly increased light levels (Table 5a). During the dry season, neither herbicide nor cattle affected light levels. Herbicide application significantly decreased relative soil moisture content during the first wet and following dry season. During the second wet season, cattle significantly increased light levels. Relative soil moisture was not affected by either factor during this time period.

Bulk density was significantly different between cattle and no cattle plots 16 months after experimental plots had been established (Table 5b). The presence of cattle significantly increased bulk density, with the

Table 5a
Effects of herbicide and cattle on the light environment (global site factor) and relative soil moisture content (%) within experimental plots in Panama throughout two wet seasons and one dry season

Treatment	Wet season 2002		Dry season 2003		Wet season 2003	
	Light (GSF)	Soil moisture (%)	Light (GSF)	Soil moisture (%)	Light (GSF)	Soil moisture (%)
C_+H_+	0.94 (0.03)	19.37 (1.71)	0.94 (0.03)	9.02 (1.28)	0.84 (0.15)	19.86 (2.38)
C_+H_0	0.85 (0.14)	19.81 (2.05)	0.94 (0.03)	9.25 (1.40)	0.84 (0.14)	19.97 (2.32)
C_0H_+	0.93 (0.04)	19.37 (1.88)	0.93 (0.04)	8.91 (1.38)	0.67 (0.20)	19.77 (2.78)
C_0H_0	0.79 (0.13)	20.4 (1.66)	0.93 (0.04)	9.63 (1.47)	0.75 (0.13)	20.46 (2.95)
Factor						
Cattle						
F	9.88	0.85	2.2	0.27	24	0.18
p-Value	0.005	ns	ns	ns	0.000001	ns
Herbicide						
F	77.23	5.11	0.03	3.75	1.35	0.74
p-Value	0.00001	0.05	ns	0.05	ns	ns
Interaction						
F	7.78	0.84	0.27	1	0.75	0.39
p-Value	0.01	ns	ns	ns	ns	ns

Mean values for light and soil moisture by treatment are reported. *F* values and significance values for two-way analysis of variance of light and soil moisture are given. C_+H_+: cattle and herbicide application; C_+H_0: cattle and no herbicide application; C_0H_+: cattle exclusion and herbicide application; C_0H_0: cattle exclusion and no herbicide application; ns: not significant.

Table 5b
Soil bulk density, soil pH, and soil cation exchange capacity (CEC) mean values within experimental plots are reported

Treatment	CEC	PH	Bulk density
C_+H_+	21.4 (2.1)	6.25 (0.34)	1.07 (0.13)
C_+H_0	20.83 (2.1)	6.33 (0.22)	0.98 (0.13)
C_0H_+	22.15 (1.9)	6.31 (0.31)	0.92 (0.11)
C_0H_0	21.78 (1.8)	6.38 (0.34)	0.91 (0.11)
Factor			
Cattle			
F	2.77	0.49	8.07
p-Value	ns	ns	0.01
Herbicide			
F	0.91	0.89	1.94
p-Value	ns	ns	ns
Interaction			
F	0.04	0.002	0.8
p-Value	ns	ns	ns

F values and significance values for two-way analysis of variance of measured soil variables are given. C_+H_+: cattle and herbicide application; C_+H_0: cattle and no herbicide application; C_0H_+: cattle exclusion and herbicide application; C_0H_0: cattle exclusion and no herbicide application; ns: not significant.

greatest bulk density in treatments with herbicide application and cattle (Table 5b). Cation exchange capacity and pH of the soil were unaffected by treatments.

5. Discussion

5.1. Species comparison

Dry tropical forests are composed of many more deciduous species than wetter forests (Murphy and Lugo, 1986). Evergreen species are more susceptible to desiccation as exemplified in this study by *Copaifera aromatica*. This slow-growing species suffered high mortality rates during the 5-month dry season. *Enterolobium cyclocarpum* differs from *C. aromatica* in that it is a fast-growing, deciduous species, commonly found in pasture environments. In our study, *E. cyclocarpum* initially had lower mortality rates than *Cedrela odorata*. However, this pattern changed after 13 months when the rodent, *S. hispidus*, foraged on the roots of many of the *E. cyclocarpum* seedlings. *Cedrela odorata* seedlings were rarely browsed upon by cattle and never excavated by rodents.

In addition to lower mortality rates, *C. odorata* had greater root collar diameter growth rates, dry mass values and leaf area values than *E. cyclocarpum*, suggesting it to be more robust in pasture environments within this region. Height increments of *C. odorata* in the control treatments over 16 months (μ = 78 cm) were similar to growth rates of *C. odorata* planted in pastures and secondary and primary forest in wet tropical forests of Mexico (μ = 86 cm) (Ricker et al., 2000).

Cedrela odorata is susceptible to mahogany shoot-borer, *Hypsipyla grandella* which destroys growing shoots, retards growth and causes forking, thereby negating their timber value (Rodgers et al., 1995). *Hypsipyla grandella* attacked less than half of the seedlings and the attacks did not result in seedling mortality at 28 months. Consequently, *C. odorata* may still serve as effective tree elements within the landscape. Further study is needed over a longer-term period to support these findings.

5.2. Experimental treatments

Many experimental studies have found that a pre-planting herbicide application increased growth rates of planted tree seedlings (Perie and Munson, 2000; George and Brennan, 2002; Shiver and Martin, 2002; Edwards et al., 2004, McInnis et al., 2004). Other plantation studies have found that cattle can either increase or decrease growth rates of tree seedlings depending on the system and stocking rates (Pitt et al., 1998; Karl and Doescher, 1993; Ramirez-Marcial, 2003). In this study, herbicide application and cattle exclusion had positive effects on the growth and survival of planted tree seedlings.

Herbicide application had a positive and significant effect on all measured variables of *C. odorata*. Light levels were significantly higher in herbicided plots than within non-herbicided plots during the first growing season, which positively affected growth and survival of both seedlings. Cattle exclusion had a positive and significant effect on all measured variables for *E. cyclocarpum*. As shown by the interaction term, in the presence of cattle, herbicide application had a significantly negative effect on growth of *E. cyclocarpum*. Topsoil erosion was noticeably more of a problem in this treatment (C_+H_+), which also had the highest bulk density (1.07 g/cm^3). In addition, the removal of other vegetation may have resulted in planted seedlings representing a greater proportion of the existing vegetation, increasing *E. cyclocarpum* susceptibility to cattle herbivory.

We suggest differences between species were caused by cattle browse preference and seed size. Cattle negatively affected both species, though only *E. cyclocarpum* was heavily browsed upon. Cattle forage on fresh stems and leaves of *E. cyclocarpum* and avoid bitter-tasting *C. odorata*. In addition, we speculate that herbicide had a greater effect on *C. odorata* because *E. cyclocarpum* relied upon seed reserves whereas small-seeded *C. odorata* could not depend on this resource. Herbicide application allowed *C. odorata* a head-start in the early stages of development, while in non-herbicided plots, *C. odorata* had a disadvantage at the initial stages of seedling development.

The positive effect of herbicide on *C. odorata* was not supported by Gerhardt's (1993) study in a dry tropical region where growth and survival of *C. odorata* was worse in vegetation removal plots. Overall, *C. odorata* growth rates were much lower in the Costa Rican study with height increments averaging 7.5 cm in control plots during the first 6 months (Gerhardt, 1993) as compared to this study where *C. odorata* height increments averaged 25.0 cm in the first 6 months. This may be due to differences in precipitation and topographic position. Whereas the Costa Rica site was flat and water-logged during the rainy season, the Panama site was hilly and well-drained.

6. Conclusions

Planting can effectively introduce certain tree species into pastures but specific treatments are required for successful establishment. *Cedrela odorata* had greater growth with herbicide application; *Enterolobium cyclocarpum* had the greatest growth with cattle removal. However, herbicide application alone was not sufficient. The greatest seedling success was seen when the two factors (C_0H_+) were combined. This management application will most likely increase the success of deciduous species used in enrichment planting within pasture environments in dry tropical regions. The order of declining preference for management applications for these species are; (1) exclude cattle and apply herbicide (C_0H_+); (2) exclude cattle and do not apply herbicide (C_0H_0); or (3) do not exclude cattle or apply herbicide (C_+H_0). This study demonstrates that species autecological characteristics need to be carefully reviewed. Planting and selection needs to be specific to the reforestation circumstance at hand.

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