



Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama

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Abstract

We conducted a silvicultural experiment to evaluate the effects of lianas on the stem diameter growth of *Prioria copaifera* (cativo), a valuable timber tree in Panama. *Dalbergia browniei*, a leguminous liana, is abundant in many riverine *P. copaifera*-dominated swamp forests in Panama's easternmost province of Darien, particularly in logged areas. In a forest along the Balsas River, *P. copaifera* dominated the forest with 96.6% of the total arboreal basal area of 34.8 m² ha⁻¹ (trees ≥ 10 cm dbh) while *D. browniei* comprised 96.9% of the total liana basal area of 3.4 m² ha⁻¹ (stems ≥ 1 cm dbh). After classifying liana infestation as severe or minor for the crown of every tree ≥ 4 cm dbh in six 25 m × 25 m plots, we cut all lianas in three randomly chosen plots. Prior to treatment 53% of trees were severely infested, 31% had minor infestation, and 16% were liana-free. During the 5 years after treatment, mean annual diameter growth of cativo trees doubled in plots where all lianas were cut compared to control plots, regardless of severity of prior liana infestation. *Prioria* regeneration was scarce in heavily vine-infested forest compared to nearby permanent plots in forest with low liana infestation. At a cost of only 16 person-hours ha⁻¹, these results suggest that a small investment in cutting lianas can greatly increase wood production in degraded cativo forests.

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Keywords: Cativo; *Dalbergia browniei*; Regeneration; Silviculture; Tree growth

1. Introduction

The abundance and ecological roles of lianas in tropical forests have long attracted the attention of tropical silviculturists (Fox, 1968; Appanah and Putz, 1984; Chaplin, 1985; Putz, 1991; Vidal et al., 1997; Carse et al., 2000). Because lianas are a major component of woody plant diversity and provide important food sources for wildlife, they play critical roles in the maintenance of biological diversity (Nabe-Nielsen, 2001; Burnham, 2002; Schnitzer and Bongers, 2002). Unfortunately, where sustainable forest management

is the primary tool for forest conservation and the primary objective is timber production, lianas can be a major impediment. Given that the likelihood of forest conversion to more profitable land uses than forestry is enhanced if prospects for subsequent timber harvests are not economically competitive, liana proliferation can contribute indirectly to forest loss.

The large trees that provide the timber value of a forest are more likely to be infested with lianas than smaller trees (Putz, 1984; Putz and Chai, 1987; Nabe-Nielsen, 2001; Perez-Salicrup et al., 2001), and lianas can have various silvicultural implications for forest management. During harvesting operations for example, felling of liana-laden trees can induce excessive stand damage because their crowns are likely to be

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connected to their neighbors (Pntz, 1984). Avoidance of this accessory damage has frequently, but not always (Parren and Bongers, 2001) been accomplished through pre-felling liana cutting (Fox, 1968; Appanah and Putz, 1984; Johns et al., 1996). An additional benefit of pre-felling liana cutting is the post-harvest reduction in liana proliferation in logging gaps (Alvira, 2004; Gerwing and Vidal, 2002). Reducing post-logging liana infestations is desirable because lianas can seriously impede succession in gaps (Schnitzer et al., 2000) and diminish opportunities for rapid recruitment and growth of desirable timber species. In addition to physically impeding establishment of seedlings and saplings of tree species in logging gaps, lianas can reduce host tree fecundity (Stevens, 1987), lowering the reproductive output of valuable timber species in forests where natural regeneration is the only cost-effective silvicultural option for stand perpetuation. Heavy liana infestations can also substantially reduce diameter growth of adult trees (Whigham, 1984; Gerwing, 2001; Clark and Clark, 1990), which lowers the net present value of future timber yields by prolonging cutting cycles.

Prioria copaifera (hereafter “cativo”, Fabaceae), a canopy tree found in freshwater wetland forests from Nicaragua to Colombia, has been exploited for timber for decades (Barbour, 1952), with little apparent concern for long-term management. Today, commercial stands are found principally in eastern Panama and northwest Colombia. Repeated logging of monodominant cativo stands during 40 years of exploitation testifies to the regenerative capacity of the species. Nevertheless, large areas of cativo forest have been converted to agricultural production or to mixed-species secondary forest and liana tangles as a result of overharvesting. Of the original 363,000 ha of cativo in Colombia for example, less than 90,000 ha remain (Linares Prieto, 1987). Similarly, extensive stands of cativo were once found in western as well as eastern Panama, but today commercial stands are found only in Darien Province. Of 30,000 ha of cativo-dominated forest in Darien in 1987 (INRENARE, 1987), an estimated 15,000 ha remained in 1999 (ANAM, 1999). Increasingly, Panamanian foresters as well as local Darien community members desire to promote sustainable logging of the remaining cativo forests.

The stands of almost pure cativo that are found as bands along the principal rivers of Darien vary between

100 m and 1 km in width. Behind the forest, treeless wetlands composed of the palms *Elaeis oleifera* and *Oenocarpus mapora* and various lianas including *Dalbergia brownei*, *Combretum sambuensis*, *Elachyptera floribunda*, *Tetrapteris macrocarpa*, *Allamanda cathartica*, *Phryganocydia corymbosa*, *Cydista diversifolia*, *Smilax spinosa*, *Banisteriopsis* spp., and *Heteropteris* spp. often dominate the landscape. In the absence of silvicultural interventions other than logging, high-statured riverine forests are likely to be converted into palm- and liana-dominated vegetation.

Present day stand structure of many riverine cativo forests in Darien is a result of traditional logging methods that do not employ heavy machinery (Grauel and Pineda, 2001). Instead, logs are levered or rolled by hand towards the river on roads constructed from 15 to 30 cm dbh (diameter at breast height, 1.3 m) cativo trunks cut and laid end to end to form two parallel rails. In many riverine cativo forests, the combination of removing all harvestable-size trees as well as many subcanopy individuals for rail building has left a very discontinuous canopy and large multiple-tree gaps, which are habitats favorable for liana proliferation.

The leguminous liana *D. brownei* proliferates abundantly in disturbed cativo forests. A principal component of the treeless wetlands found behind the natural river levees where cativo dominates, this liana uses cativo forest edges to climb into the forest canopy. Although this species does not establish in the deep shade of the cativo forest understory, large stems (up to 20 cm diameter) are commonly found hanging from the 30–40 m high canopy in many of the cativo forests of the lower Balsas, Samba, and Tnira Rivers (Grauel and Pineda, 2001). Areas with high liana densities seem to have developed in large logging gaps created 20–30 years ago. Many mature cativo trees in heavily infested areas are visibly deformed, apparently from having developed while carrying large liana loads or from having been damaged during logging. In other areas that have been continually and recently subjected to small-scale harvesting, *D. brownei* is proliferating on the ground in large canopy gaps and appears to delay cativo regeneration. In the present study we measured, by observation and experimental liana removal, the effect of lianas on cativo adult stem growth as well as on seedling height growth, recruitment, and mortality.

2. Study site

The study was conducted in a riverine cativo forest along the Balsas River in eastern Panama (8°07'N, 77°52'W). Mean annual precipitation at Camoganti, the nearest town (approximately 8 km from the study site), is 2457 mm (based on Government of Panama published reports for 1978–1982, 1984, 1986, and 1988–1994) while rainfall measured at the study site in 1998 and 1999 totaled 2970 and 2758 mm, respectively. The forest is inundated periodically with rainwater during the 9-month wet season from April to December. In addition, it is flooded twice per day for about 5 days during the monthly spring tides known locally as the 'aguaje'. The freshwater backup caused by the Pacific spring tides affects the riverine forests as far as Camoganti, 73 km from the mouth of the Tuira River at the Gulf of San Miguel. Although at the study site the tidal flooding is mostly the freshwater backup, soil samples show a slight brackishness (electrical conductivity 5.0 mmho cm⁻¹), and mangrove forests are found only 7 km downriver from the study site. Soils at the study site are heavy clays classified in the suborders fluvent and aquept, are acidic to slightly acidic, and poorly drained (Tapia, 1999).

The study site is on private land owned by a logger and is next to an operating sawmill. The owner, who has been logging cativo in Darien since 1960, is currently logging further upriver and has protected the forest where the study took place because he values it for hunting and aesthetics, although he told us that he had harvested a few scattered trees about 10 years prior to the study. This cativo forest is composed of about 95% *P. copaifera* of all size classes (Grauel and Kursar, 1999). Other tree species include *Pterocarpus officinalis*, *Mora oleifera*, and *Carapa guianensis*. Results from a 1 ha permanent plot show 10 cativo trees ha⁻¹ ≥60 cm dbh, the legal cutting limit, but the majority of these were left due to bad form or hollowness. Regeneration of cativo of all sizes is abundant.

3. Methods

In September 1997 six 25 m × 25 m plots were installed in a line at 50–75 m intervals in areas with intact canopies but with relatively high densities of lianas compared to the forest overall. Each plot was

subdivided into twenty-five 25 m² subplots to facilitate stem mapping. Inside the plots we measured all trees ≥4 cm dbh as well as the diameters of all ascending liana stems ≥1 cm at breast height. We did not attempt to differentiate genetically distinct lianas; every stem encountered at 1.3 m above the ground was measured. To increase the sample size for the growth analyses of cativo, additional trees were measured up to 5 m outside of each plot, but no lianas were measured outside the plots. Every plant was tagged and mapped and subsequent censuses were carried out in 1998, 1999, and 2001. For the growth analysis, diameter classes for trees were selected based on relative canopy position; 15 cm dbh was used as the cutoff between canopy and understory individuals. Due to the low canopy of the forest where lianas are abundant, even trees 15–30 cm dbh may receive substantial direct illumination, while trees <15 cm dbh are generally in the understory.

During the initial measurements, each tree was classified as severely or lightly infested by lianas. Severely infested trees had at least five individual liana stems hanging from the crown and some stems or branches apparently deformed by lianas. Lightly infested trees had fewer than five liana stems hanging from the crown and no visible deformations. For the growth analyses, growth rates of liana-free trees were included in the lightly infested category. All lianas were cut with a machete inside and up to 10 m outside of three randomly chosen plots.

In 10 randomly chosen 25 m² subplots in each plot, all natural regeneration of cativo from seedlings to small trees 1 cm in diameter were counted, tagged, and measured (height) before the vine cutting treatment and 2 years later. Where necessary to reduce heteroskedasticity, seedling frequency data were natural log-transformed. Mean relative height growth for seedlings in treated and control plots was compared with a two-sample *t*-test and the difference of mean absolute height growth was tested by ANOVA using initial height as a covariate. Mortality of these seedlings and small trees in treatment and control plots was also compared. Two years after the initial census, the same subplots were surveyed for new cativo regeneration. Treatment differences in mean density of seedlings recruited per plot was compared with *t*-tests.

For several reasons, including the observation that increases in cross sectional area of lianas are associated with much larger increases in leaf area than in

trees (Putz, 1983), it is desirable to estimate diameter growth rates of lianas. In 2001, 4 years after the initial measurements, 56 *D. brownnei* lianas in the control plots were again measured to estimate stem diameter growth. Individuals <6 cm dbh were measured with dial calipers; a mean diameter was calculated from measurements of the long and short axes. Lianas ≥ 6 cm dbh were measured with a diameter tape. Wood density was estimated using 10 bark-free stem samples, to allow comparisons with other studies. While growth rates of trees are often negatively correlated with wood density, this pattern may not hold for lianas that do not produce structural wood for support.

Canopy openness above 2 m was measured immediately before and 2 months after liana cutting in all plots with a vertical densitometer (Stumpf, 1993). Both measurements were made during the rainy season. This instrument projects a point vertically upward that encounters either canopy or open sky at each evenly spaced sample point along a linear transect. Canopy openness is estimated as the proportion of points of open sky along three transects in each plot.

To compare rates of cativo growth and regeneration in heavily vine-infested areas with forest with low liana infestation, data from the six plots of the present study were compared with data from plots selected at random for a demographic study of cativo in the same forest. The demographic study was based on five 20 m \times 20 m and five 40 m \times 40 m plots established in March 1997. All trees ≥ 10 cm dbh were tagged, mapped, and measured (dbh), while trees ≥ 1 cm dbh were measured in all five 20 m \times 20 m plots and in five randomly chosen 20 m \times 20 m subplots in each of the 40 m \times 40 m plots. All trees were measured annually from 1997 to 2001. In addition, all trees <1 cm dbh in eight randomly chosen 5 m \times 5 m subplots of each plot were tagged and mapped and were measured (height only) in November 1997. This population of seedlings and saplings was censused approximately every 2 months for 2 years whereas height was measured annually.

4. Results

4.1. Canopy openness

Two months after cutting lianas, significant but modest increases in canopy openness were observed

in the treated plots. There was no difference in the before and after canopy coverage in the three control plots, while the three treated plots showed a mean increase of 7% ($P < 0.01$) in canopy openness.

4.2. Liana growth

Mean annual diameter growth of *D. brownnei* was 1.3 mm per year ($n = 56$, S.D. = 1.4, range = -0.8 to 5.5 mm). Mean wood density of *D. brownnei* (dry weight/fresh volume) based on 10 samples was 0.38 g cm^{-3} (S.D. = 0.047).

4.3. Forest structure

Based on the mean number of stems ≥ 4 cm from the six 25 m \times 25 m plots, cativo dominated the forest with 1320 stems ha^{-1} dbh (S.D. = 212), virtually identical to nearby areas of riverine forest with lower liana densities (1338 stems ha^{-1} , Grauel and Kursar, 1999). *P. officinalis*, the only other abundant tree species, was represented by 51 stems ha^{-1} ≥ 4 cm dbh. The $35.1 \text{ m}^2 \text{ ha}^{-1}$ of cativo basal area represents 96.6% of the total basal area of trees ≥ 4 cm dbh.

For all cativo trees ≥ 4 cm dbh, 71% had lianas hanging from the crowns, while 93% of mid- and upperstory trees (≥ 15 cm dbh) had lianas. There were 1757 ascending liana stems per hectare ≥ 1 cm dbh (S.D. = 270), with a mean liana basal area of $3.40 \text{ m}^2 \text{ ha}^{-1}$ (S.D. = 0.8). Of the two liana species found, *D. brownnei* comprised 96.9% of the basal area. The only other liana encountered, *E. floribunda* (Hippocrateaceae), was mainly represented by small stems, with 75% of the ascending stems <3 cm in diameter, while over 80% of the *D. brownnei* stems were ≥ 3 cm in diameter (Fig. 1).

4.4. Cativo natural regeneration

Prior to liana cutting, in the six heavily liana-infested plots the mean density of cativo seedlings and saplings (<1 cm dbh) was 707 ha^{-1} (S.D. = 1154). In contrast, in the 10 randomly located plots for the demographic study of cativo at the same site, the mean density of cativo seedlings and saplings was 6350 ha^{-1} (S.D. = 12,882, Fig. 2). Although this was almost an order of magnitude difference and is plainly discernible in the forest, variability was

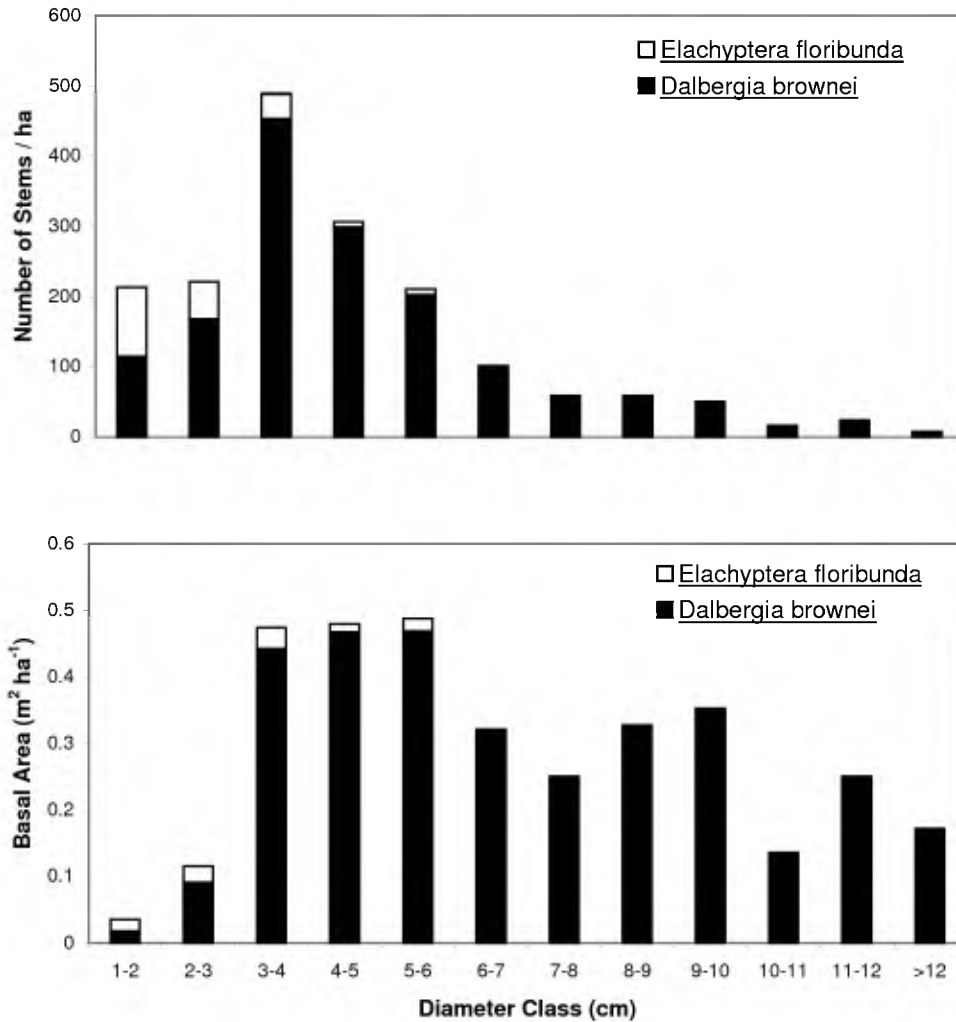


Fig. 1. Frequency and basal area of ascending lianas in six 25 m × 25 m plots in heavily infested riverine *P. copaiifera* forest degraded by repeated entry logging.

large due to the clumped distributions of seedlings, but the difference was significant ($t = 3.12$, d.f. = 14, $P = 0.008$).

For cativo regeneration present at the beginning of the study, relative and absolute height growth over 2 years did not differ between liana-cut and control plots. Although mean initial height for seedlings and saplings happened to be significantly greater in the three control than in the three treatment plots, there was no difference in initial height of only those trees that survived to produce growth records. Cativo

seedling and sapling mortality was nearly double in treated than in control plots (63% versus 36%, Pearson $\chi^2 = 6.2$, $P = 0.01$).

Cativo seedling recruitment during 2 years after liana cutting was more than three times greater in the treated than in the control subplots but, due to large variability, was not statistically significant ($t = 1.30$, d.f. = 4, $P = 0.26$, Fig. 3). On a per hectare basis, over 7700 cativo seedlings recruited during 2 years after lianas were cut compared to just over 2200 seedlings for the control plots.

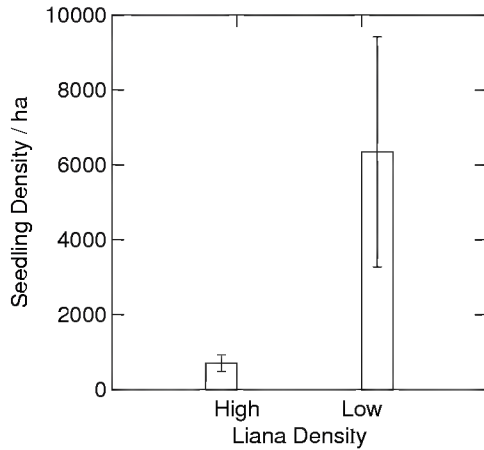


Fig. 2. Mean (± 1 S.E.) density of *P. copaifera* regeneration (<1 cm dbh) in areas of high ($N = 6$) and low ($N = 10$) liana densities.

4.5. *Cativo* growth

Mean annual diameter growth of *cativo* trees during 1997–2001 was about twice as rapid in the liana-cut compared to the control plots (Fig. 4). For trees ≥ 15 cm dbh the difference was significant ($t = 3.41$, d.f. = 4, $P = 0.03$) while for trees between 4 and 15 cm the difference was not statistically significant ($t = 2.61$, d.f. = 4, $P = 0.06$). Surprisingly, severity of liana infestation had little apparent effect (no significant differences found) on *cativo* diameter growth for either control or treated plots (Fig. 5). The largest difference

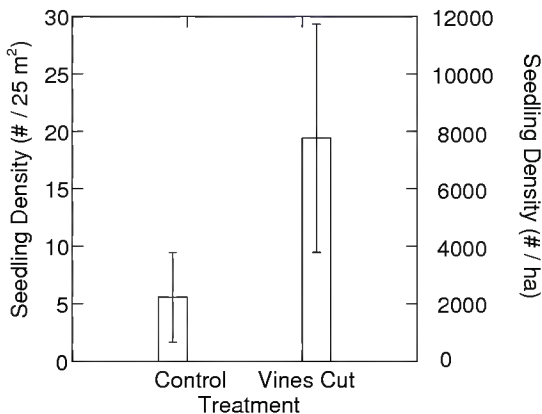


Fig. 3. Mean (± 1 S.E.) *P. copaifera* seedling recruitment censused 2 years after liana cutting in three control and three treatment plots.

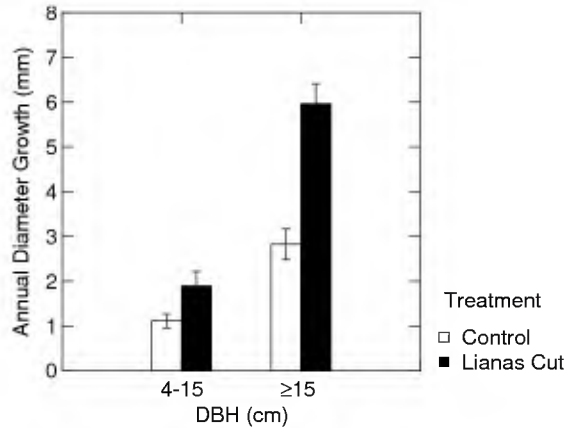


Fig. 4. Mean (± 1 S.E.) annual *P. copaifera* diameter growth based on five annual censuses of all trees ≥ 4 cm dbh in three control plots and three plots in which all lianas were cut at the beginning of the study.

was for canopy trees in the control plots, where severely infested trees grew slightly slower than lightly infested trees.

5. Discussion

5.1. Canopy openness

Despite their abundance, liana cutting had only a slight (7%) but statistically significant ($P < 0.01$) effect on canopy openness of the *cativo* forest, because most of the liana foliage is displayed on the tops of tree crowns in *cativo* forest. Liana-infested *cativo* forests look “feathery” at the top of the canopy, due to the abundant emergent branches of small-leaved *D. browni* searching for higher trellises. Two years after liana cutting, canopy openness was similar for all plots, perhaps because the *cativo* canopies increased leaf production after liana cutting. In contrast, Gerwing (2001) found that increases in canopy light transmittance persisted for 2 years following vine cutting, and Perez-Salicrup (2001) measured no change in canopy openness 4 months after vine cutting in a Bolivian lowland forest but an increase in openness 2 years later. Both the Bolivian and Brazilian studies took place in much drier forests and probably on less fertile soils than the present study; perhaps the *cativo* trees were better able to take advantage of the removal of lianas and produce foliage rapidly.

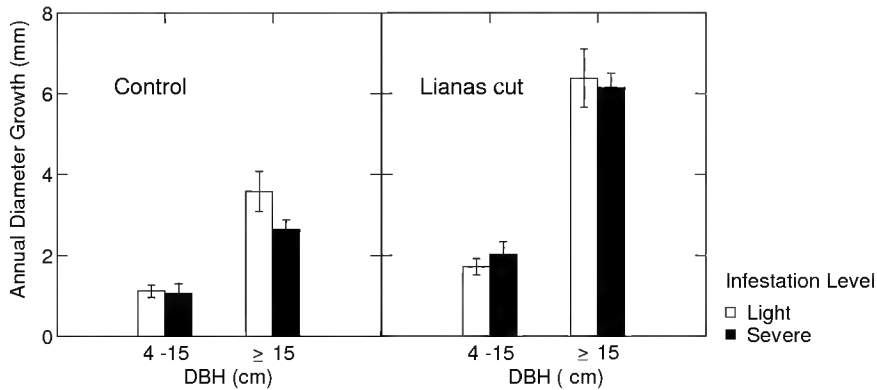


Fig. 5. Mean (± 1 S.E.) annual *P. copaifera* diameter growth of cativo based on five annual censuses according to liana infestation level in control and treatment plots.

5.2. Liana growth

The low diameter growth rate of *D. browniei* is similar to the growth rate found by Putz (1990, 1.4 mm per year) for 15 liana species from a tropical moist forest in Panama. In a lowland wet forest in Ecuador the most abundant liana, *Machaerium cuspidatum*, had an average annual growth rate of 1.4 mm per year for stems between 30 and 50 mm (Nabe-Nielsen, 2002). In contrast to these low diameter growth rates, a single shoot of *D. browniei* was observed to grow 1.24 m in length in 71 days.

5.3. Cativo natural regeneration

Increased mortality of cativo seedlings in liana-cut plots compared to control plots appeared to be due to numerous large liana stems falling from the canopy, most within the first year following cutting. In addition, floodwaters commonly move coarse woody material around on the forest floor, which frequently results in the bending and breakage of seedlings. This additional impact may explain why tree seedling mortality increased significantly following liana cutting here but not in a tropical tierra firme forest in Bolivia with higher liana densities (Perez-Salicrup, 2001).

Enhanced seedling recruitment in liana-cut plots (Fig. 3) more than compensated for increased mortality of the initially scarce regeneration in these heavily liana-infested areas. Large cativo seed crops were produced in 1997 and 1999, and the germinated

seedlings from the May–June 1999 seedfall were captured in the plot census in November 1999 before dry season (January–April) mortality occurred. Three possible mechanisms for this increased seedling recruitment following liana removal include: (1) reduced seed movement out of the liana-cut plots; (2) enhanced seedling survival; (3) increased seed production.

Reduced seed movement could result because cativo seeds are large (mean fresh weight = 48 g, Lopez, 2001) and mainly dispersed by water. Seeds that fall and that are not partially buried in the heavy wet soil may be transported by the monthly spring tides or the periodic flooding caused by wet season rains. Fallen liana stems could have acted as small dams inhibiting cativo seed movement during inundation.

If seed production and retention as well as capture of water dispersed seeds were equal in all plots, high early mortality rates in the control plots would explain the difference in seedling densities between control and treatment plots. But most cativo seedling mortality occurs during the short dry season from January to April (Lopez, 2002), and the plots were censused after seedfall but before the onset of the dry season of the second year after liana cutting.

Catavo trees newly liberated from lianas may have produced more seeds. A possible mechanism that could help explain an increased production of seeds by cativo is that lianas interfere with cativo flower or seed production, either physically or through competition for light. *D. browniei* produces long recurved

spines that wrap around small diameter objects that they encounter, such as flower-bearing branches. A drain on host resources caused by the constriction of vascular elements in branches or twigs was proposed by Stevens (1987) to explain the negative effect of lianas on the fecundity of *Bursera simaruba* trees in Costa Rica, and a similar mechanism may be at work in the cativo/*Dalbergia* canopy. Another possible mechanism for the proposed increased seed production in the treated plots is the removal of belowground competition after the death of the lianas, resulting in increased nutrient availability. Increased water availability may also have been a factor, since seasonally flooded cativo forests can experience severe short-term annual droughts. Putz (1991) suggests that because lianas do not need to produce large diameter structural roots, root systems of lianas may be more efficient in water and nutrient uptake. Lianas were also experimentally shown to be effective belowground competitors in a study with north temperate vine species (Dillenburg et al., 1993).

5.4. Cativo growth

Although liana cutting resulted in a notable positive increase in *P. copaiifera* stem diameter growth, lianas may not be solely responsible for low forest-wide growth rates, as proposed by Gerwing (2001) for a seasonal Amazonian forest in Brazil. In the riverine cativo swamps in Panama discussed in this study, mean annual growth of trees in the control plots was not significantly different than similar-sized trees in the nearby permanent plots where lianas were generally less abundant (data not shown).

Mean annual growth of cativo trees of all sizes in both treatment and control plots was greatest during

the second year following liana cutting and then declined (Table 1). Although the liana leaves fell during the first 2 months after cutting and the hanging stems fell within the first year following treatment, this pattern of increased growth followed by decline is probably not due to a fertilizer effect from the fallen liana material; forest-wide growth rates for cativo, based on permanent plots at this site and three others in different watersheds in Darien Province, showed the same pattern, suggesting a correlation with climate.

The observation that the growth rates of liana-infested control plot trees ≥ 15 cm dbh did not differ from growth rates of trees of the same dbh in adjacent permanent plots with few lianas (data not shown) could be attributed to the lower overall canopy height in the area of the liana-cutting plots. With fewer large trees in the liana-abundant areas of the forest, trees that otherwise would be subcanopy individuals may receive more light than a similar-sized tree in adjacent non-liana forest. This interpretation suggests that these liana-abundant areas are old canopy gaps in the process of recovery, similar to the “vine-dominated disclimax” of Whigham (1984) or the “stalled gap” of Schnitzer et al. (2000).

The profound negative effect of lianas on cativo growth and reproduction probably results from a combination of aboveground and belowground influences. Lianas were estimated to occupy 31% of the forest canopy surface area during the wet season in a seasonally dry tierra firme forest in central Panama (Avalos and Mulkey, 1999) and liana leaves might significantly reduce light availability for cativo leaves. Belowground competition for nutrients and water in the dry season could also be a factor. Given that rooting depth in cativo forests is limited by the high

Table 1
Mean (± 1 S.E.) annual diameter growth (mm) of *P. copaiifera* 1, 2, and 2–4 years after liana cutting

Treatment	Liana infestation	1997–1998		1998–1999		1999–2001	
		N	Mean annual increment (mm)	N	Mean annual increment (mm)	N	Mean annual increment (mm)
Control	Light	171	1.5 (0.2)	168	2.2 (0.3)	152	1.6 (0.2)
	Severe	204	1.6 (0.2)	196	3.1 (0.3)	181	1.8 (0.2)
Lianas cut	Light	166	2.2 (0.2)	164	4.1 (0.4)	144	2.7 (0.3)
	Severe	180	3.3 (0.3)	172	6.6 (0.4)	154	4.5 (0.3)

water table (Lopez, 2002), belowground competition for water may be severe during the dry season because root systems die back during wet season flooding (Lopez, 2002). In a semi-deciduous lowland forest in Bolivia, Perez-Salicrup and Barker (2000) found significantly less negative water potentials in *Senna multijuga* trees where lianas were cut as well as increased tree diameter growth. In contrast, in the same forest after liana cutting, Barker and Perez-Salicrup (2000) found no difference in water status of mahogany trees with and without lianas and concluded that lianas and trees had access to different sources of water due to different rooting depths.

Two issues pertinent to considerations of liana cutting as a silvicultural tool are cost of implementation and biodiversity impacts. Based on the experimental plots, it would require 16 person-hours to treat 1 ha of forest. Although the experiment took place on private land, the majority of these degraded forests are on state land managed by the Panamanian Environmental Ministry (ANAM). Currently, ANAM is working with several communities in Darien to develop a partnership whereby forest areas are identified for potential timber production and legal tenure is transferred to local community groups. The government intends to train community members in mapping, inventory, and other management activities; liana cutting could be one of the recommended silvicultural treatments.

Conservation of biodiversity is a critical issue in our study area, especially because of the presence of Darien National Park and the current improvement of the Pan-American highway that will doubtlessly increase colonization rates and forest clearing. Liana-cutting in seasonally flooded cativo forests is not expected to have severe effects on species diversity for several reasons. Tree species diversity is extremely low in tidally-flooded cativo forests (Grauel and Kursar, 1999) and only one species of liana seems to have proliferated excessively as a result of several decades of uncontrolled timber exploitation. Because this species, *D. brownei*, is also a common component of nearby treeless wetlands, attempts at controlling its proliferation in cativo forests suited for timber production probably will never eliminate it. Promoting sustainable management of cativo forests for timber production could actually serve as a biodiversity conservation tool. By providing local communities

with viable economic activities in the areas surrounding Darien National Park, pressure to exploit the natural resources of the park could be reduced.

Acknowledgements

The authors thank Ruperto Molina for the generous access to his land for research and Liduvina Quiroz and Carmen Galdames for liana identification. Martin Barker provided useful comments on an earlier version of the manuscript. This work was funded by the International Tropical Timber Organization. Logistical support was provided by ANAM, Autoridad Nacional del Ambiente, and the Smithsonian Tropical Research Institute.

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