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Forest Ecology and Management 162 (2002) 197–208

Forest Ecology
and
Management

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Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest

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Received 26 November 2000; accepted 10 February 2001

Abstract

We examined the effect of disturbances of varying intensity on the dominant modes of regeneration among woody plants in tropical dry forest in lowland Bolivia. Seed survival and density, mortality, height, crown area, and basal diameters of seedlings and sprouts were compared among four treatments of varying disturbance intensity (high-intensity burn, low-intensity burn, plant removal, and harvesting gap) over a period of 18 months following treatments. High- and low-intensity burns reduced densities of viable seed by an average of 94 and 50%, respectively. Tree seedlings were more abundant than tree sprouts in all treatments. There were few differences in seedling density among treatments. Sprouts were most common in the plant removal and low-intensity burn treatments than in harvesting gap and high-intensity burn treatments. Seedling mortality was higher than sprout mortality during the first year following treatments. Sprouts were taller, had more stems per individual, larger crown areas, and larger basal diameters than seedlings. Origin of sprout differed among treatments. Eighteen months following treatments, 85% of individuals >2.5 m tall were sprouts. Most seedlings >2.5 m tall after 18 months had established in high-intensity burn treatments. Sprouting individuals dominated regeneration after all treatments, however, in high-intensity burn treatments, sprouts were relatively less dominant due to smaller sprouts and larger seedlings after high-intensity burns. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Dry tropical forests; Sprouting; Disturbance intensity; Species composition; Bolivia; Fire; Prescribed burns

1. Introduction

Patterns of forest regeneration following natural or anthropogenic disturbances are determined by interactions between the disturbance regime (i.e., intensity, frequency, scale) and the biologies of species (i.e., life history, physiology, behavior; Pickett and White,

1985). Modes of regeneration, i.e., from sprouts, seedling banks, seed banks, or dispersed seeds, may influence the success or dominance of a species in successional communities. Consequently, shifts in species composition following disturbances can arise from differences in species-specific modes of persistence through these disturbances. In this study, we examine the effect of disturbance intensity on modes of regeneration in a tropical dry forest in lowland Bolivia.

The importance of sprouting as a means of survival varies within a site as well among forest types,

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depending on the intensity of disturbance. Several studies show that frequency of sprouting declines with increasing severity of disturbance. For example, in both wet and dry tropical forests, sprouts were less common after slash burning than after less intense disturbances (Sampiao, 1995; Miller and Kauffman, 1998a,b; Kauffman, 1991; Uhl et al., 1981; Uhl and Jordan, 1984). Regeneration from seed may also be affected by disturbance intensity. While less intense disturbances such as canopy opening may stimulate many seeds to germinate (e.g., Vazquez-Yanes and Orozco-Segovia, 1993), more severe disturbances, such as intense fires, kill seeds buried in surface soils (Brinkmann and Vieira, 1971; Uhl et al., 1981). Therefore, it is often colonizing species that regenerate via widely dispersed seeds that dominate following disturbances of high intensity (Uhl et al., 1981; Schimmel and Granstrom, 1996).

Modes of regeneration not only determine survival through a disturbance, but also influence growth and survival following disturbance. Due to their larger carbohydrate reserves, sprouts may form larger, taller crowns more rapidly than seedlings (Miller and Kauffman, 1998b). And, although few studies have directly compared survival of seedlings and sprouts, their survival rates are also likely to differ. While mortality of both seedlings and sprouts may be affected by herbivores (Moreno and Oechel, 1994) or fungal pathogens (Wenger, 1953; Augspurger, 1983), mortality of seedlings is more dependent on external factors such as light availability (Veenendall et al., 1995; Thompson et al., 1998; Kitajima, 1994) and soil moisture (Gerhardt, 1996). Sprout mortality, at least initially, is correlated with internal factors such as the size or age of the original stem, height and extent of stem damage, and number of sprouts sharing the same root system (Wenger, 1953; Blake, 1983).

In this study, we characterized early successional patterns following canopy opening, plant removal, and controlled burns of high and low intensity in a tropical dry forest in lowland Bolivia. This particular forest region has been commercially managed for timber by the Chiquitano indigenous group since 1982 (McDaniel, 2000). Of the 17 timber species that are harvested from these forests, more than half are shade-intolerant and do not have sufficient regeneration following selective logging to sustain future yields. Fire, of both natural and anthropogenic origins, has

likely been a pervasive influence on these dry forests (Kennard, 2000), and therefore, forest managers have begun to explore prescribed burning as a silvicultural tool to enhance the regeneration of these shade-intolerant species.

This study is part of a larger project that examined the effects of fire intensity on soils, commercial tree regeneration, and plant diversity (Kennard, 2000). In this paper, we describe the effect of disturbance intensity on the dominance of alternate regeneration modes (i.e., from seed or by sprouting). We define dominance by various measures of size, including height, diameter, and crown area, rather than basal area.

2. Methods

2.1. Study site

This study was conducted in the Lomerio Community-owned Forest, Province of Nuflo de Chavez, Department of Santa Cruz, Bolivia (16°45'S, 61°45'W). Lomerio is situated in the heart of Chiquitania, which lies in the transition zone between the humid forests on the southern rim of the Amazon basin and the thorn scrub formations of the Gran Chaco. The natural vegetation is classified as tropical dry forest (*sensu* Holdridge, 1967). The regional climate is characterized by a strong dry season from May to October. The mean annual temperature at Conception is 24.3 °C with temperatures that vary between 3 °C (July) and 38.1 °C (October, Killeen et al., 1990). Mean annual precipitation is 1129 mm. The landscape is dominated by low hills composed of granite, gneiss, and metamorphic rocks of Precambrian origin (Geobold, 1981) punctuated by exposed granitic outcrops (*inselbergs*). The soils of the area are classified as Inceptisols and Oxisols (Iporre, 1996). Elevation varies between 400 and 600 m a.s.l. Canopies of mature forest range from 12 to 18 m tall and are dominated by trees of the Leguminosae (60% of total basal area of trees >10 cm dbh); trees in the families Bignoniaceae, Anacardiaceae, and Bombacaceae are also abundant (Killeen et al., 1998). Understory trees are mostly represented by the families Sapindaceae and Myrtaceae. A spiny ground bromeliad, *Pseudananas sagenarius*, is distributed

over approximately 80% of the forest and occurs in clumps up to 2000 m² (MacDonald et al., 1998).

Lomerio consists of 27 Chiquitano communities with a total population of approximately 5000. The Chiquitanos of Lomerio have been managing their forests for timber since 1982 with technical and financial support from several international institutions (e.g., APCOB, BOLFOR). This study was conducted in a management unit near the community of Las Trancas that was selectively harvested in 1997 (harvesting intensity of 4.4 m³ ha⁻¹).

2.2. Experimental design and treatments

In June 1997, 16 recently formed felling gaps meeting the following criteria were located for study: canopy gap area between 200 and 600 m², slopes no greater than 15°, less than 20% rock outcrops, no trees >40 cm DBH within gap area, and not located in the path of skid trails. Each gap was divided into four 10 m × 10 m plots by cardinal axes originating from the gap center. Existing gap area was enlarged to a uniform 20 m × 20 m area by cutting all vegetation >2 m tall (*sensu* Brokaw, 1985) by machete or chainsaw. One of the four treatments was randomly assigned to each 10 m × 10 m plot within each gap: (1) high-intensity burn; (2) low-intensity burn;

(3) above-ground plant and coarse debris removal (hereafter referred to as plant removal); (4) a gap control (Fig. 1). Other than cutting all vegetation >2 m tall, vegetation and woody debris in the gap control was not manipulated. In the plant removal and low-intensity burn treatments, all vegetation was cut at or near the soil surface and everything ≥2.5 cm diameter was removed and distributed as evenly as possible in the high-intensity burn treatment. Therefore, after fuels were manipulated and before prescribed burns, the plant removal and low-intensity burn treatments had similar amounts of litter and woody debris and no above-ground vegetation. Pre-burn fuel loads in high-intensity burn treatment subplots ranged from 10.8 to 82.8 kg/m² and averaged 48 ± 4.9 kg/m² (mean ± 1 S.E.). Almost half of this mass was comprised of fuels >7.5 cm diameter. Fuel loads in the low-intensity burn treatment subplots ranged from 0.8 to 4 kg/m² and averaged 2.2 ± 2.3 kg/m². Sixty-six per cent of the fuel mass in low-intensity plots was fine fuel, <6 mm diameter.

Slash was left for five rainless weeks to dry and prescribed burns were conducted from 29 August to 1 September 1997, near the end of the 5-month dry season and before peak seed fall. A circular ignition technique was used for both burn treatments. Maximum soil temperature during burns was measured

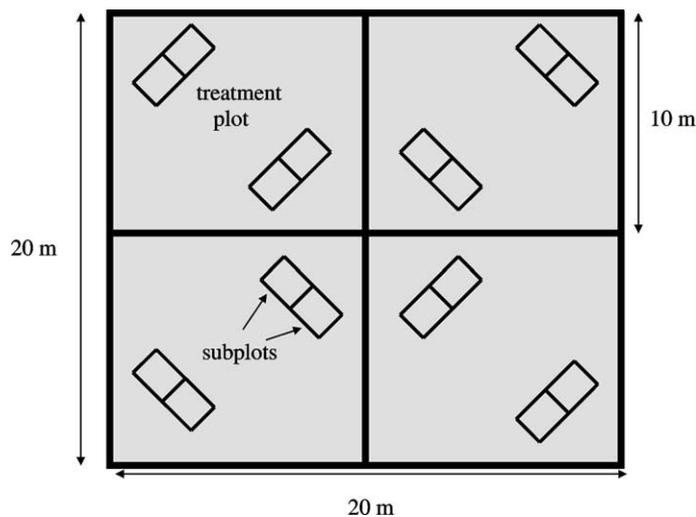


Fig. 1. Experimental design of treatment blocks. Each block consists of a 20 m × 20 m felling gap partitioned into four 10 m × 10 m treatment plots. Each treatment plot was randomly assigned to one of the four treatments: gap control, plant removal, low-intensity or high-intensity burns. Within each treatment plot, two permanent sampling subplots (2 × 2 each) were located near the gap center and two additional subplots near the gap edge. Sixteen blocks were used for each of the parameters examined ($n = 16$).

at 0 and 3 cm depths using temperature indicating paints (Tempilaq[®], Tempil Division, Air Liquide America Corporation, South Plainfield, NJ). Fire intensity was estimated by Beaufait (1966) technique which calculates total energy output from the amount of water vaporized from cans during burns as

$$\begin{aligned} \text{Total energy output} = & [(80 \text{ cal/g water}) \times (\text{g water})] \\ & + [(540 \text{ cal/g water} \\ & \times (\text{g water})] \end{aligned}$$

where 80 cal are needed to raise each gram of water from 20 °C to the boiling point and 540 cal are needed to vaporize each gram of water. Two cans were placed on the soil surface of each burn plot. Depth of water was measured immediately before each burn and within 24 h after. To account for the amount of water lost due to evaporation, two cans were placed in the center of an unburned gap and the amount of water evaporated within 24 h measured.

Three weeks following burns, four permanent subplots (2 m × 2 m each) were established in each treatment plot, two located near the gap center and two located near the gap edge (Fig. 1). These permanent subplots were used for sampling seedling/sprout density and size. Destructive sampling techniques (i.e., soil seed bank samples) were conducted in the treatment areas outside the 4 m² subplots.

2.3. Soil seed banks and seed rain

We compared treatment effects on the survival of seeds stored in soil at the time of treatments. The week following controlled burns, four seed bank samples (20 cm × 20 cm, 3 cm depth) were collected from each gap treatment plot in each block, spread on 10 cm × 50 cm trays, watered twice daily, and examined every 7–10 days for germinated seeds. Trays received direct sunlight during the morning and evening hours. After 11 weeks, all seedlings were collected and pressed. The total number of germinated seeds were compared among treatments using ANOVA with treatments as fixed effects and blocks as random effects followed by Tukey's HSD post-hoc comparisons.

We quantified seed rain following controlled burns using two seed traps per gap, placed 2.5 and 7.5 m from gap centers, respectively, and an additional trap

located 20–25 m from each gap in the forest understory. Traps were constructed of 50 cm × 50 cm PVC frames with a net of woven plastic sewn to the sides, and elevated 50 cm above the soil surface with stakes. Seeds were collected every 7–10 days for 9 weeks following burns, counted, and identified to species or morphospecies. The total number of seeds, commercial tree seeds, liana seeds, and species were compared among trap locations (gap center, gap edge, and forest understory) using ANOVAs with trap location as a fixed effect and blocks as random effects followed by Tukey's HSD post-hoc comparisons.

2.4. Seedling and sprout density and mortality

Seedlings have been variously defined as individuals still dependent on seed reserves (e.g., Garwood, 1983), to individuals up to 2.7 m tall (Whitmore, 1984). In this study, we did not use size or physiology as a defining character, rather we define seedlings as individuals originating from seed as opposed to those regenerating as sprouts. Tree seedling and sprout densities were measured in two subplots per treatment 3, 6, 9, and 12 months following controlled burns. At each sampling period, all commercial tree species within subplots were identified as sprouts or seedlings and tagged to assess mortality. Distributions of seedling and sprout densities could not be normalized and therefore were compared among treatments using Kruskal–Wallis non-parametric tests. Mortality of seedlings and sprouts was assessed by calculating killing power, a parameter similar to mortality rate, as

$$k = (\log_{10} A_x - \log_{10} A_{x+1})$$

where A_x represents the number of individuals in the first cohort following treatments, and A_{x+1} the number of these individuals surviving into the next year (Begon and Mortimer, 1981). Killing power was calculated separately for four tree species that were represented by both seedlings and sprouts.

2.5. Seedling and sprout size

Seedling and sprout sizes were compared 9 months following controlled burns. In the two center subplots of each gap treatment, the five tallest individuals from of each of the following groups were selected for measurements: tree sprouts, tree seedlings, liana

sprouts, and liana seedlings. For each individual, height, basal diameter, crown length (L), and crown width (W) were measured. Additionally, for sprouting individuals, the number of stems, diameter of the largest sprout, and sprout origin (root, root collar, or stem) were measured. Crown areas were estimated as $\text{Area} = \frac{1}{4}L \times W \times 3.1416$

Crown widths and lengths were difficult to measure for lianas that had one-to-many long climbing or scrambling stems. For these lianas, the measurement of crown length (L) was estimated by multiplying the number of stems by the estimated average length of these stems. The average width of leaves on stems was used as crown width (W).

The sizes of seedlings and sprouts were compared using ANOVAs with treatment, regeneration mode, and lifeform as factors. For these tests, mean heights, crown areas, stem diameters, and numbers of stems were log transformed prior to analyses. Blocks were treated as a random effect in each model. To compare the origin of sprouting (root, root collar, stem) among treatments, frequencies of each were compared among gap treatments using Kruskal–Wallis tests.

2.6. Dominant species, lifeforms, and regeneration modes among treatments

To identify which species, life forms, and regeneration modes were dominant in each treatment, all individuals within each 100 m² treatment plot >2.5 m tall were identified at 9 and 18 months, their mode of regeneration (seedling or sprout) determined, and heights measured. The total number of individuals >2.5 m tall were compared among treatments using a Kruskal–Wallis test at 9 months and an ANOVA at 18 months. The proportions of tree seedlings, tree sprouts, liana seedlings, and liana sprouts among the total number of individuals >2.5 m tall were compared among treatments using a Kruskal–Wallis test.

3. Results

3.1. Controlled burn temperature and intensity

Temperatures at the soil surface during high-intensity burns averaged 704 ± 42 °C ($x \pm \text{S.E.}$, $n = 16$). The highest temperature measured was 927 °C. Temperature

at 3 cm depth averaged 227 ± 27 °C ($n = 16$). Fire intensities ranged from 152 to 3795 kcal and averaged 1627 ± 241 kcal ($n = 15$). Flame heights ranged from 1.5 to 5 m.

Temperatures at the soil surface during low-intensity burns averaged 225 ± 33 °C ($n = 12$); the highest temperature measured was 413 °C. Elevated temperatures at 3 cm were only detected in two of the 16 plots; these averaged 107 ± 7 °C ($n = 2$). Fire intensity ranged from 22 to 68 kcal and averaged 41 ± 3 kcal ($n = 15$). Flame heights were low, ranging from 10 to 50 cm.

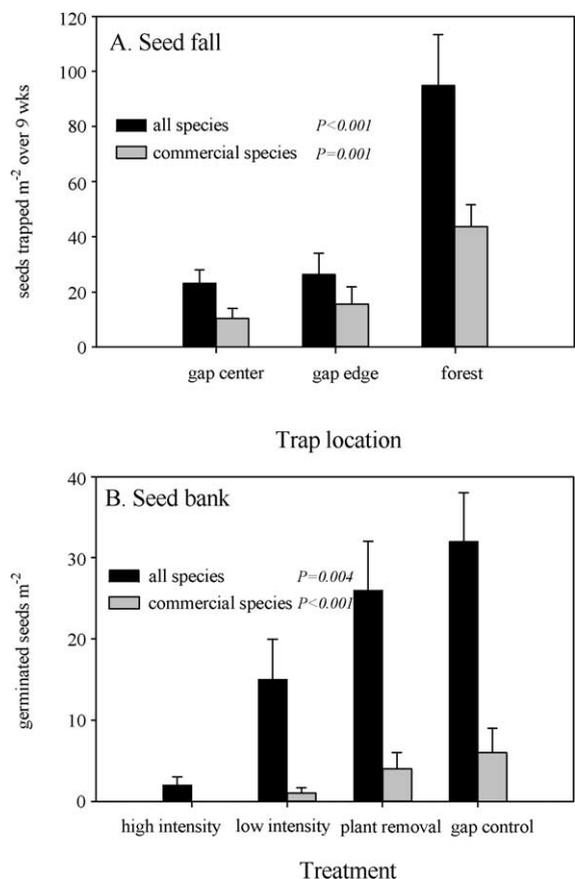


Fig. 2. (A) Total number of seeds and number of commercial tree seeds captured in 0.25 m² seed traps placed in forest, gap center, and gap edges for 9 weeks following treatments. (B) Density of viable seeds of all species and of commercial tree species in seed banks sampled to 3 cm depth in four treatments immediately following controlled burns. P -values are results of ANOVAs testing for differences among trap location (A) or treatment (B). Bars represent standard errors ($n = 16$).

3.2. Seed bank and seed rain studies

Density of germinants was highest in seed banks sampled from gap controls and lowest in high-intensity burn plots (Fig. 2). An average of 32 (5–164) seeds per square meter germinated in seed banks sampled from gap controls. In seed banks sampled from high-intensity burn plots, only five germinants were found in all 64 seed bank samples (representing a total area of 2.56 m²). *Ruellia* spp. (Acanthaceae), perennial herbs, were the most common species germinating in seed banks sampled from gap control, plant removal, and low-intensity burn treatments.

An average of 94 (24–212) seeds per square meter were caught by forest seed traps during the 9-week collection period from 11 September to 13 November 1997. Seed rain peaked the first week of October, but by the third week, it had fallen to two seeds per square meter per week. Seed rain into gaps was only 25% of that collected in forest traps (Fig. 2). Roughly equal number of seeds fell into gap center and gap edge traps. *Anadenanthera colubrina*, a commercial tree species, had the most abundant seed fall. Of the total 181 *Anadenanthera* seeds collected, 77% fell into forest traps, 14% into gap edge traps, and 9% into gap center traps. Distribution of *Astronium urundueva* seed rain, also a commercial tree species, was more even; of the total 94 *Astronium* seeds collected, 29% fell in gap center traps, 35% into gap edge traps, and

36% into forest traps. *Thiloua paraguariensis* (Combrataceae), a colonizing vine, had the most abundant seed rain of vines; of the total 154 seeds collected, 66% fell into forest traps, 12% into gap edge traps, and 21% into gap center traps.

3.3. Density and mortality of seedlings and sprouts

Overall, tree seedlings were more abundant than tree sprouts (Fig. 3, Table 1). Among treatments, tree seedlings were most abundant in gap control plots 3 months after controlled burns. There were no significant differences in seedling density among treatments at 6, 9, and 12 months. Sprouts were most abundant in the plant removal treatment and low-intensity burn treatments at 3, 6, 9, and 12 months. Overall, mortality was greater among seedlings than sprouts among the four tree species examined (Table 2).

3.4. Sizes of seedlings and sprouts

Tree and liana sprouts were taller ($F = 8.9$, $P = 0.003$), had more stems per individual ($F = 32.1$, $P < 0.001$), larger crown areas ($F = 42.8$, $P < 0.001$), and larger basal diameters ($F = 13.4$, $P < 0.001$; Fig. 4) than tree and liana seedlings. Among sprouts, the origin of sprouting differed among treatments (Fig. 5). Sprouting from roots was more common in burned plots ($P < 0.001$, $\chi^2 = 25.2$), sprouting from

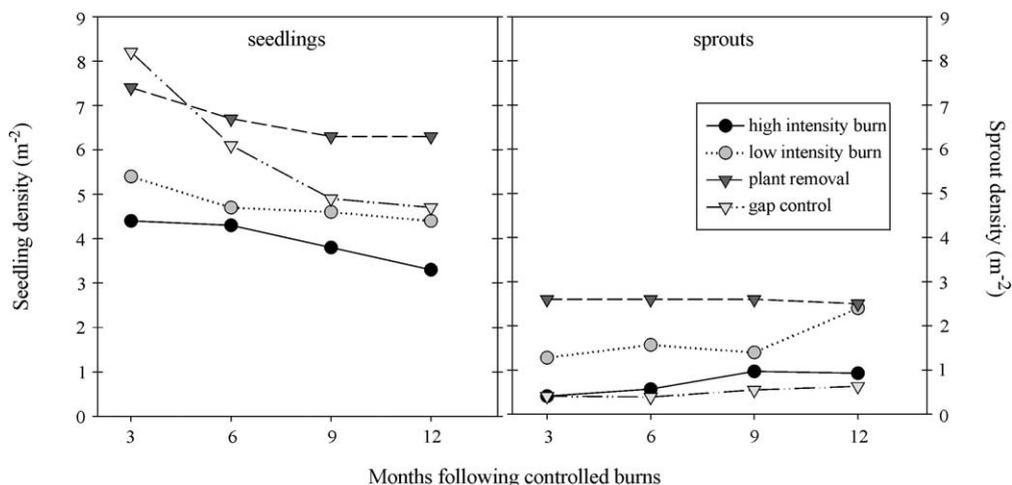


Fig. 3. Mean density of commercial tree seedlings and sprouts in high-intensity burn, low-intensity burn, plant removal, and gap controls at 3, 6, 9, and 12 months following burns ($n = 16$). Both graphs follow the same legend.

Table 1

Results of Kruskal–Wallis tests comparing the density of commercial tree seedlings and sprouts in gap, plant removal, low-intensity burn, and high-intensity burn treatments after 3, 6, 9, and 12 months

Months	Densities compared among seedlings and sprouts (d.f. = 1)		Densities compared among treatments (d.f. = 3)			
	χ^2	<i>P</i>	Seedlings		Sprouts	
			χ^2	<i>P</i>	χ^2	<i>P</i>
3	44.7	<0.0001	8.1	0.045	15.2	0.002
6	33.8	<0.0001	5	0.17	16.1	0.001
9	20.5	<0.0001	3.6	0.31	17.7	0.001
12	21.9	<0.0001	4.2	0.25	15.4	0.002

the root collar was more common in the low-intensity burn and plant removal treatments ($P < 0.001$, $\chi^2 = 23.8$), and sprouting from stems was the more common in the plant removal and gap control plots ($P < 0.001$, $\chi^2 = 23.8$).

3.5. Individuals >2.5 m tall in 100 m² treatment plots

Nine months following treatments, 100% of individuals >2.5 m tall were sprouts. Of these sprouts, 90% were trees, the remaining 10% were lianas. The

plant removal treatment had the most individuals >2.5 m, with 3 per 100 m² ($\chi^2 = 8.8$, $P = 0.03$). Eighteen months following treatments, sprouts comprised approximately 85% of all individuals >2.5 m tall. Among the seedlings that did attain heights >2.5 m by 18 months, most had established in high-intensity burn treatments. The number of individuals >2.5 m tall did not differ among treatments ($F = 0.8$, $P = 0.50$). The most common individuals >2.5 m tall were root sprouts of the commercial tree *Centrolobium microchaete* (Fig. 6). The second most common

Table 2

Killing power (*k*), a parameter similar to mortality rate, for four commercial tree species in the four gap treatments during the first year following controlled burns. Higher *k* indicates higher mortality during a given period. The number of individuals that died during this period are listed in columns “#”

Species	High-intensity burn		Low-intensity burn		Plant removal		Gap control		All individuals	
	<i>k</i>	#	<i>k</i>	#	<i>k</i>	#	<i>k</i>	#	<i>k</i>	#
<i>Aspidosperma</i>										
Seedlings	0.20	3	0.30	1	0.30	1	0.60	3	0.25	10
Resprouts	0.00	0	0.22	9	0.05	1	0.48	4	0.17	15
<i>Caesalpinia</i>										
Seedlings	0.00	0	0.00	0	0.07	1	0.22	2	0.09	3
Resprouts	0.00	0	0.11	2	0.00	0	0.06	1	0.05	3
<i>Centrolobium</i>										
Seedlings	0.11	2	0.12	4	0.06	1	^a	1	0.14	10
Resprouts	0.18	2	0.00	0	0.11	2	0.12	1	0.07	5
<i>Copaifera</i>										
Seedlings	0.09	3	0.10	2	0.09	6	0.06	4	0.09	20
Resprouts	0.00	0	0.00	0	0.08	1	0.00	0	0.02	1
<i>Astronium</i>										
Seedlings	0.11	10	0.13	9	0.18	9	^a	1	0.14	29

^a Where A_{x+1} was equal to 0 (all individuals died), *k* equals infinity.

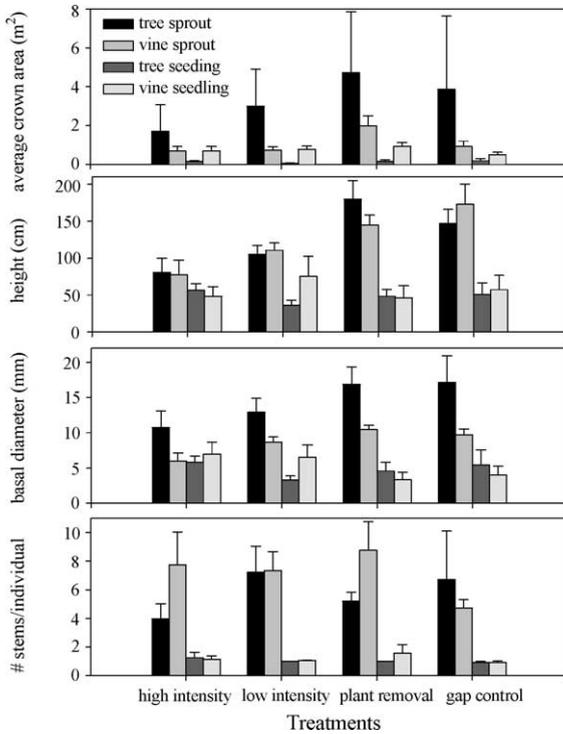


Fig. 4. Average crown areas, heights, basal diameters of the largest new stem, and number of stems per individual of tree seedlings, vine seedlings, tree sprouts, and vine sprouts in each treatment 9 months following controlled burns.

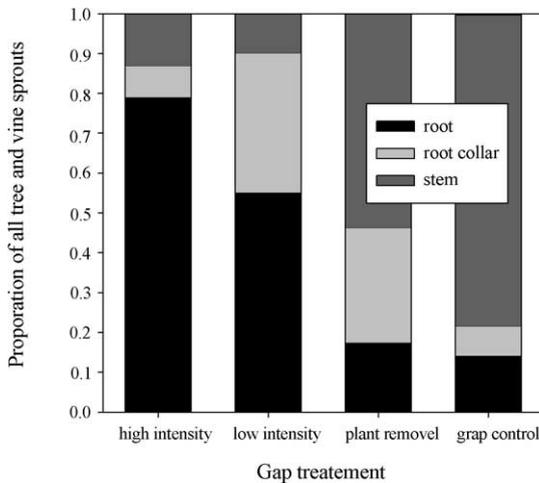


Fig. 5. Proportion of all sprouting individuals sprouting from roots, root collars, or stems in high-intensity burn, low-intensity burn, plant removal, and gap controls 9 months following burns.

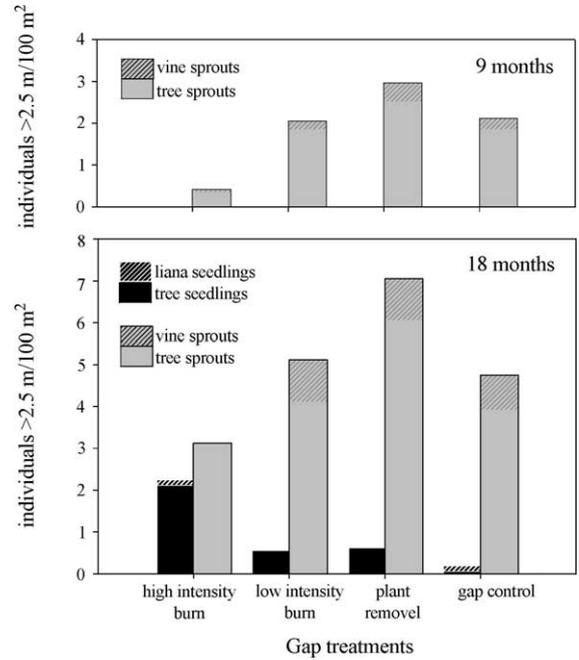


Fig. 6. Number of individuals >2.5 m tall in each 100 m² gap treatment plot after 9 and 18 months. Individuals are divided into classes based on regeneration mode (seedling or sprout) and life form (tree or liana).

species >2.5 m tall was *Mimosa* sp., also found predominately as a sprout. *A. colubrina*, the third most abundant species, was found predominately as seedlings. Other common species whose seedlings reached heights >2.5 m tall were the trees *Trema micrantha*, *Heliocarpus* sp., and *A. urundueva*, and the vine *T. paraguariensis*.

4. Discussion

4.1. Seed survival and dispersal

High soil temperatures created by high-intensity burns, well above the temperature range known to kill seeds (e.g., Brinkmann and Vieira, 1971; Uhl et al., 1981; Probert, 1992), reduced densities of viable seed by an average of 94%. The high mortality of seeds stored in soil implies that seedling regeneration after high-intensity burns was mostly limited to seeds dispersed after burns. In fact, common species in high-intensity burn plots, *A. colubrina*, *A. urundueva*, and

T. paraguariensis, were species frequently caught in gap seed traps. In low-intensity burns, density of viable seed was only reduced by approximately half that of gap controls. This higher seed survival may reflect the greater heterogeneity of low-intensity burns or it may reflect survival of seeds buried below the soil surface. In low-intensity burn plots, establishing seedlings may have originated either from seed banks or seeds dispersed following burns.

4.2. Dominance of sprouts

Although establishing from seed was a more common mode of regeneration following the gap control, plant removal, low- and high-intensity burn treatments, regeneration in these four treatments was dominated by sprouts, i.e., sprouts occupied a greater volume of available growing space. This dominance of sprouts was due to their overall larger size; sprouts were taller, had larger crown areas, larger basal diameters, and more stems than seedlings in all gap treatments. Very similar results were reported by Miller and Kauffman (1998b) who compared the size of tree seedlings and sprouts after slashing and burning of a tropical deciduous forest in Mexico. In their study, they found sprout height, crown area, stem diameter, and number of stems were also significantly greater than for seedlings. Miller and Kauffman (1998b) attributed the larger sizes of sprouts to their larger carbohydrate reserves. Sprouts, which draw carbohydrates from pre-established root systems, have much larger carbohydrate reserves than seedlings, which are limited to seed reserves. In our study, many of the sprouts measured appeared to be seedling sprouts, i.e., sprouts originating from a seedling-sized individual. Even root systems of seedling sprouts may provide larger carbohydrate reserves than provided by seeds, particularly in dry forests where most seeds are wind dispersed and necessarily small (Gentry, 1995) and established root systems are proportionately larger than in wetter forests (Cuevas, 1995). At this study site, e.g., storage taproots were observed in three month-old *Anadenanthera* seedlings.

Sprouts may still have an advantage over seedlings even after both have depleted their carbohydrate reserves. The larger root system of sprouts would offer more surface area for water and nutrient uptake and likely extend deeper into the soil than seedling root

systems. This difference would confer an advantage to sprouts, particularly in dry forests where water is seasonally limiting. This study was conducted during an El Niño period, and the onset of the rainy season was delayed for several months. This may partly explain the lower mortality rates of sprouts we observed, although a more detailed comparison of the water relations of seedlings and sprouts would be necessary to confirm this. Other causes of mortality, such as fungal pathogens, low light availability, stem damage, size or age of the original stem, were not specifically examined in this study and deserve further attention.

4.3. Changes in relative dominance of sprouts among treatments

Although sprouts were larger than seedlings in all treatments, the magnitude of this difference was dependent on treatment intensity. For example, while the average height of sprouts was roughly three times the average height of seedlings in the unburned treatments, sprouts were only slightly taller than seedlings in the high-intensity burn treatment (Fig. 4). This general pattern is also apparent for crown area and stem diameter. The shift in relative dominance among sprouts and seedlings in high-intensity burn plots is particularly apparent among individuals >2.5 m tall. In high-intensity burn plots, seedlings comprised 40% of individuals >2.5 m tall, whereas in the gap control, plant removal, and low-intensity burn treatments, only 10% of individuals >2.5 m tall were seedlings.

The decrease in dominance of sprouts in high-intensity burn plots was partly due to lower sprout densities and smaller sprouts in this treatment. Plant cell death during fires depends on both the maximum temperature and duration of heating; fire intensity, therefore, is an important determinate of the survival of sprouting tissue. Often, a greater number of plants of increasingly larger size are killed at higher fire intensities (Moreno and Oechel, 1994). Intense fires may also hinder growth of sprouts by killing part of the root system, thereby decreasing total carbohydrate reserves. A decrease in sprout size and density following intense fires has been reported in several studies conducted in tropical forests. For example, Sampiao (1995) studied the effects of fire intensity on

coppicing of caatinga vegetation in Brazil and found that the sprouts were both smaller and less abundant in areas that experienced more intense fires. Similarly, Kauffman (1991) found decreasing frequency of sprouting and slower sprout growth in areas of greater fire intensity in moist forests in the Brazilian Amazon.

The decrease in dominance of sprouts is also partially due to the greater size of seedlings in high-intensity burn plots. More seedlings reached heights >2.5 m in high-intensity burn plots than in other treatments. Most of these seedlings >2.5 m were shade-intolerant tree species establishing from seeds dispersed after the experimental burns, i.e., *Anadenanthera* and *Astronium*. Relative growth rates of these two species were greatest in high-intensity burn plots (Kennard, 2000), presumably due to both increased soil nutrients and decreased competition.

4.4. Differences in dominant species among treatments

In addition to alteration in the relative dominance of sprouts, disturbance intensity also appeared to influence which species were dominant in post-treatment regeneration. While gap, plant removal, and low-intensity burn treatments were dominated by species present before treatments (present either as seedlings/saplings or as seeds stored in soil seed banks), high-intensity burn treatments were comparatively more dominated by species that were dispersed into gaps following controlled burns. For example, herb cover in gap control, plant removal, and low-intensity burn plots was dominated by several species in the genus *Ruellia* (Acanthaceae), the most common germinants in seed banks sampled from these treatments. *Ruellia* spp. comprised a much smaller fraction of the herb cover in high-intensity burn plots, likely due to seed mortality during burns. Herb cover in high-intensity burn plots was largely composed of annual herbs, particularly species of Asteraceae.

The dominant woody vine species in the gap control, plant removal, and low-intensity burn treatments was *Mimosa* sp., perhaps more correctly called a scrambling shrub because it is free standing up to heights of 5 m and only then begins to support its limbs on branches of adjacent trees. It appears that *Mimosa* sp. does not survive fires of high-intensity, as it was infrequent in high-intensity burn plots in our

study. Instead, vine cover in high-intensity burn plots was dominated by a liana species that regenerated primarily from seed, *T. paraguariensis* (Combretaceae). Seeds of *Thiloo* were the most abundant of any vine species caught in seed traps following burns. This species was also abundant in an area of Lomerio previously burned by a wildfire (Mostacedo et al., 1999).

The pattern among tree species was similar to that of herbs and vines. In the gap control, plant removal, and low-intensity burn treatments, dominant species were mostly those that regenerated primarily by sprouting from stems present before treatments (e.g., *Acosmium cardenasii*, *Casearia gossypiosperma*, *Acacia lorentensis*, *Casaeria arborea*, *Neea hermaphrodita*). All of these species are non-commercial tree species. In high-intensity burn plots where most advanced regeneration was killed, *A. colubrina* and *A. urundueva*, commercial tree species whose seeds were dispersed following burns, were the among the most dominant tree species. A notable exception to this pattern is *C. microchaete*, the most common tree species >2.5 m tall. *Centrolobium* regenerated predominately as suckers from the root system of damaged or harvested mature trees, and was found in all treatments, including high-intensity burns. High-intensity burns may favor species with dormant buds below-ground, either on roots or below-ground stems. Sprouting from root tissue was the most frequent means of vegetative reproduction in high-intensity burns, likely due to the protection of below-ground buds by the insulating properties of soil.

5. Management implications

At this dry forest site, disturbance intensity was an important factor influencing the composition of regeneration by influencing alternate modes of persistence. Although regeneration from seed was the most common mode of regeneration, post-disturbance communities were dominated by sprouting vegetation due to the larger size of sprouts. Only after the most intense disturbance, high-intensity fire, did individuals arising from seed compare in size to sprouting individuals.

Differences in modes of regeneration among disturbances of varying intensity are important for understanding patterns of forest structure and development

in Lomerio. Several lines of evidence point to the occurrence of past disturbance in the Lomerio forests. The even-aged size class structures, dominance of long-lived pioneers, and presence of charcoal and pottery shards in soils suggest the present day forests formed after severe disturbances, possibly fire of anthropogenic origins (Kennard, 2000). Dendrochronology of *Cedrela fissilis*, one of the few species that creates annual rings, indicated that intense fires have occurred roughly every 30–60 years in Lomerio (J. Huffman, personal communication). The apparently high sprouting capacity of the woody plant community may be the consequence of a historically extensive disturbance regime.

These results have serious implications for silvicultural treatments that aim to improve regeneration from seed of commercial tree species. In the gap control, plant removal, and low-intensity burn treatments, commercial trees were dominated by sprouts of non-commercial trees present before gap formation. Only in the high-intensity burn treatment were individuals of commercial tree species dominant. Although high-intensity burns resulted in the most vigorous regeneration of commercial tree seedlings, this treatment also altered community structure and composition more drastically than the other treatments, and therefore should be used with great caution in naturally managed forests.

Acknowledgements

This work was funded by BOLFOR (Proyecto de Manejo Forestal Sostenible), Santa Cruz, Bolivia. Field work was conducted in the Las Trancas community-owned forest, Lomerio. E. Stone, K. Kitajima, G. Tanner, T. Fredericksen, and J. McDaniel provided constructive comments on an earlier draft. We thank J. McDaniel, L. MacDonald, J. Chuviru, K. Heuberger, N. Fredericksen, J. Justiniano, J. Pesoa, J. Faldin, and numerous additional Chiquitano community members for assisting with fieldwork.

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