Commercial tree regeneration 6 years after high-intensity burns in a seasonally dry forest in Bolivia

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Abstract: The effects of three site-preparation treatments (high-intensity burn, low-intensity burn, and mechanical cleaning with machetes and chainsaws) on the regeneration of commercial tree species, composition and structure of competing vegetation, and soil chemical and structural properties were evaluated in a seasonally dry forest in southeast Bolivia. Six years after controlled burns, the high-intensity burn treatment had both the highest density and the tallest individuals of shade-intolerant commercial tree species. Competing vegetation was also less dominant in the high-intensity burn treatment relative to other treatments. However, high-intensity burns were not beneficial for commercial tree species with shade-tolerant or intermediate regeneration. Soil analyses revealed that certain changes in soil texture and soil chemistry (e.g., Ca and Mg concentrations and cation exchange capacity) caused by high-intensity burns persisted 6 years after the fires. These findings confirm that this suite of shade-intolerant commercial species requires very intense disturbances for their regeneration. However, several ecological, economic, and social barriers currently preclude the management-scale application of prescribed fire in Bolivia. More research is needed on cost-effective treatments to improve regeneration.

Résumé : Les effets de trois traitements de préparation de terrain (brûlage de forte intensité, brûlage de faible intensité et dégagement mécanique avec des machettes et des scies à chaînes) sur la régénération des espèces commerciales d'arbres, la composition et la structure de la végétation compétitrice ainsi que sur les propriétés chimiques et structurales du sol ont été évalués dans une forêt du sud-est de la Bolivie où il existe une saison sèche. Six ans après les brûlages dirigés, le brûlage de forte intensité a produit la plus forte densité et les plus hauts arbres dans le cas des espèces commerciales de lumière. La végétation compétitrice a également été mieux contrôlée par le brûlage de forte intensité que par les autres traitements. Cependant, le brûlage de forte intensité n'a pas été bénéfique pour les espèces commerciales dont la régénération est intermédiaire ou tolérante à l'ombre. Les analyses de sol ont révélé que certains changements dans la texture et la chimie du sol (concentration de Ca et de Mg, capacité d'échange cationique) causés par le brûlage de forte intensité ont persisté pendant six ans après le passage du feu. Ces résultats confirment que ce groupe d'espèces commerciales de lumière requiert de très fortes perturbations pour se régénérer. Cependant, plusieurs contraintes écologiques, économiques et sociales empêchent présentement l'utilisation du brûlage dirigé pour des fins d'aménagement en Bolivie. D'autres travaux de recherche sont nécessaires pour mettre au point des traitements rentables afin d'améliorer la régénération.

[Traduit par la Rédaction]

Introduction

The Chiquitania region in eastern Bolivia, one of the largest and most diverse tropical dry forests in the neotropics (Gentry 1993; Killeen et al. 1998), is becoming increasingly endangered by a rapid expansion in industrial agriculture and settlement (Dinerstein et al. 1995). Consequently, there has been a growing interest on the part of the Bolivian government to discourage the conversion of forests to competing, non-forest land uses by fostering natural forest management practices (Nittler and Nash 1999). In most managed dry forests in this region, however, sustainable management is threatened by a distinct lack of regeneration among valuable timber species (Mostacedo et al. 1999; Pinard et al. 1999) (Table 1). A lack of seed sources as a result of previous overharvesting may account for this scarcity, but poor regeneration also plagues tree species that have only recently been harvested (Fredericksen 1999; Mostacedo et al. 1999). Part of the problem is that the majority of commercial timber species in this region are shade intolerant and likely require more intense and large-scale disturbances for their establishment than those created by selective logging practices (Fredericksen 1998; Pinard et al. 1999). Options for increasing regeneration of shade-intolerant commercial species are complicated by high levels of competing vegetation, particularly lianas, that quickly colonize following large-scale disturbances (Fredericksen 1998; Mostacedo et al. 1999).

In the 1990s, forest managers in Bolivia identified prescribed fire as a potential tool for increasing the regeneration of shade-intolerant commercial species. Evidence has suggested that fire, of both natural and anthropogenic origins, has a pervasive influence on dry Bolivian forests (Pinard and Huffman 1997; Gould et al. 2002; Kennard 2002). Prescribed burns produce several effects that are beneficial for the regeneration of these species, including vegetation and

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Table 1. Market value, adult and sapling rarity in mature unharvested forest, and shade tolerance of 19 commercial tree species of the seasonally dry forests of southeast Bolivia (Pinard et al. 1999).

Species	Timber value	Adult rarity[a]	Sapling rarity[b]	Shade tolerance[c]
Amburana cearensis	High	3	3	1
Anadenanthera colubrina	Low	1	2	1
Aspidosperma cylindrocarpon	Low	2	3	2
Aspidosperma rigidum	Low	1	2	2
Astronium urundueva	Low	2	3	1
Caesalpinia pluviosa	Low	1	2	2
Cariniana estrellensis	Low	2	2	3
Cedrela fissilis	High	3	3	1
Centrolobium microchaete	High	1	3	1
Copaifera chodatiana	Low	2	3	3
Cordia alliodora	High	3	2	1
Hymenea courbaril	Low	3	3	1
Machaerium scleroxylon	High	1	2	3
Phyllostylon rhamnoides	Low	2	2	3
Platymiscium ulei	Low	3	3	1
Schinopsis brasilensis	Low	2	3	1
Spondias mombin	Low	2	3	1
Tabebuia impetiginosa	Low	1	3	1
Tabebuia serratifolia	Low	3	3	1

Notes: Timber value is based on market value in 1999. All species listed are deciduous during the dry season in this region of Bolivia (Justiniano 1998).

[a]Adult rarity (>20 cm diameter at breast height): 1, common (> 5 trees·ha^{-1}); 2, intermediate (1–5 trees·ha^{-1}); 3, rare (<1 tree·ha^{-1}).

[b]Sapling rarity (5–10 cm diameter at breast height): 1, common (>20 trees·ha^{-1}); 2, intermediate (5–20 trees·ha^{-1}); 3, rare (<5 trees·ha^{-1}).

[c]Shade tolerance: 1, high light only, large gaps; 2, partial shade, small gaps; 3, partial or full shade only, understory.

slash removal, mineral soil exposure, and nutrient release (Hungerford et al.1990; Bond and van Wilgen 1996). As a part of this focus, a study was initiated in 1997 that examined the effects of prescribed fires of different intensities on commercial tree regeneration, forest soils, and community structure and composition (Kennard and Gholz 2001; Kennard et al. 2002; Kennard and Putz, in press). The first 18 months of regeneration revealed that controlled burns enhanced the seedling establishment, growth, and survival of certain shade-intolerant species. However, high-intensity burns also increased soil bulk density and slowed water infiltration rates. These changes in soil physical properties could inhibit seedling establishment and growth over longer periods, particularly after the initial increases observed in soil nutrients returned to background levels (Kennard and Gholz 2001). The objective of the present study was to gain a better understanding of the benefits of prescribed burning in seasonally dry forests by examining patterns of regeneration and soil nutrients 6 years after burns.

Materials and methods

Study region and sites

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. The regional climate is characterized by a strong dry season from May to October. The mean annual temperature at Concepcion, a town approximately 50 km from the study site, 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 (GEOBOL 1981), punctuated by exposed granitic outcrops (inselbergs). The soils of the area are classified as Inceptisols and Oxisols (Ippore 1996). Elevation varies between 400 and 600 m above sea level. Canopies of mature forest range from 12 to 20 m tall and are dominated by trees of the Leguminosae (60% of total basal area of trees >10 cm diameter at breast height). 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 floor (MacDonald et al. 1998). The majority of canopy trees are deciduous during the dry season (Justiniano 1998).

Experimental design and treatments

In June 1997, 12 recently formed felling gaps were opportunistically selected and enlarged to a uniform 20 m × 20 m area through the cutting of all vegetation >2 m tall (sensu Brokaw 1985), by machete or chainsaw. Each gap was divided into four 10 m × 10 m plots, and one of four treatments was randomly assigned to each 100-m^2 plot: (*i*) high-intensity burn; (*ii*) low-intensity burn; (*iii*) mechanical cleaning with machete and chainsaw (hereafter referred to as "cleaned"); and (*iv*) no removal of vegetation below 2 m in height (hereafter referred to as "gap control"). Other than all vegetation >2 m tall being cut, vegetation and woody debris in the gap control were not manipulated. In the cleaned and low-intensity burn treatments, all vegetation was cut at or near the soil surface and any slash produced that was ≥2.5 cm diameter was removed from these treatment plots and distributed as evenly as possible in the adjacent high-intensity burn treatment plot. Therefore, after fuels were manipulated and before prescribed burns were carried out, the plant removal and low-intensity burn treatments had similar amounts of litter and woody debris (<2.5 cm diameter) and no aboveground vegetation. The high-intensity burn treatment plots had roughly three times their original fuel loads. Preburn fuel loads in high-intensity burn treatment plots averaged 48 ± 4.9 kg/m^2 (mean ±1 SE), while those in low-intensity burn treatment plots averaged 2.2 ± 2.3 kg/m^2. 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 when fires are most likely to spread because of the increase in leaf litter and drier forest-floor conditions. Temperatures at the soil surface during burns averaged 704 ± 42 °C and 225 ± 33 °C (mean ± SE) in the high- and low-intensity burns, respectively (measured at two points per plot, at least 2 m from plot edges).

Commercial tree regeneration

Following prescribed burns, four permanent subplots for monitoring commercial tree regeneration (2 m × 2 m each) were established in each treatment plot, two located near the gap center and two located near the gap edge. In July 2003, 6 years after the experimental burns, all commercial tree species rooted within each 4-m^2 subplot were identified, their heights measured, and their origin determined where possible. Although all individuals were tagged in the first census in 1997, very few of these tags remained in 2003, therefore relative growth rates were not calculated. Additionally, all commercial tree species taller than 2.5 m and rooted within the 100-m^2 treatment plots were identified, their heights and basal diameter measured, and their origin (seed or sprout) determined where possible. These taller individuals were measured to characterize which commercial species were dominant or successful in regenerating gaps.

Competing vegetation

To compare the composition of competing vegetation among treatments, total vegetation cover and percent cover by life form (bromeliads, lianas, herbs, shrubs, and trees) was estimated visually >2 m and <2 m height in each 4-m^2 subplot. Maximum total cover was limited to 100%, but where leaf cover of different life forms overlapped, the sum of their percent covers could total >100%. In addition, all individuals of *Acosmium cardenasii* rooted within each 4-m^2 subplot (any height) were identified, their heights measured, and their origin determined where possible. *Acosmium cardenasii* was measured in more detail, because this species is the most abundant canopy tree in the forest and a frequent competitor of commercial trees. To identify the most dominant competitors, all individuals of noncommercial tree species taller than 2.5 m and rooted within the 100-m^2 treatment plots were identified, their heights and basal diameter measured, and their origin (seed or sprout) determined where possible.

Soil analyses

Two soil samples from 0–8 cm depth were collected and mixed thoroughly in the field, and a composite subsample was bagged for each treatment plot. Soil samples were air-dried, sieved, and stored in a cool, dry area until transported to the Laboratorio del Centro De Investigacion Agricola Tropical (Santa Cruz, Bolivia) for chemical analyses. Potassium (K), calcium (Ca), and magnesium (Mg) were extracted with Mehlich I solution (0.05 mol/L HCl and 0.0125 mol/L H_2SO_4) and analyzed by ICAP spectroscopy. Soil organic matter content was analyzed using the Walkley–Black dichromate method. Soil texture was characterized through particle-size analysis, using the hydrometer method.

Statistical analyses

Density of commercial and noncommercial trees >2.5 m tall, total cover, percent cover of trees and lianas, and all soil variables were compared among treatments. ANOVAs were used, with treatments as fixed effects and blocks as random effects, followed by Tukey's HSD post-hoc comparisons. All percentages were transformed using the arcsine transformation before analyses. Density of commercial trees and *Acosmium cardenasii* and percent cover of bromeliads, shrubs, and herbs could not be normalized and were compared among treatments using Kruskal–Wallis nonparametric tests.

Results

Commercial tree regeneration

Six years after prescribed burns, high-intensity burn plots had the highest densities of commercial tree regeneration and control plots had the lowest densities (Table 2 and Fig. 1). This pattern was also significant for *Anadenathera colubrina*, the most abundant commercial species, and *Astronium urundueva*. *Copaifera chodatiana* revealed a different pattern of regeneration; individuals of this species were most abundant in the cleaned treatment. No differences among treatments were found for *Caesalpinia pluviosa*, *Aspidosperma rigida*, and *Centrolobium microchaete*. An additional six commercial species were also found in felling gaps but at densities too low for comparison.

There were three times more commercial trees >2.5 m tall in the high-intensity burn treatment than in the other treatments ($\chi^2 = 16.2$, $p = 0.001$) (Fig. 2). Three species made up over 90% of these commercial trees in the high-intensity burn plots: *Anadenathera colubrina* (41%), *Centrolobium microchaete* (33%), and *Astronium urundueva* (16%) (Table 3). All *Anadenathera colubrina* individuals >2.5 m tall in high-intensity burn plots regenerated from seed, while 30% of individuals of this species in the other treatments were resprouts. The tallest *Anadenathera colubrina* was a 6.5-m individual found in a high-intensity burn plot. *Centrolobium microchaete*, in contrast, regenerated almost exclusively from root sprouts (true seedlings of this species were rare and all were <1 m tall). Root sprouts of *C. microchaete* were, on average, taller than the regenerating sprouts of other commercial species. The tallest *C. microchaete* was an

Table 2. Mean density (no./m^2) of commercial tree species and the most abundant noncommercial species (*Acosmium cardenasii*) among three site-preparation treatments in a Bolivian dry forest 6 years after prescribed burns.

Species	Control	Cleaned	Low-intensity burn	High-intensity burn	χ^2	p
All commercial species (12 species)	0.10 (0.04)	0.41 (0.09)	0.34 (0.07)	0.54 (0.08)	15.1	<0.001
Anadenathera colubrina	0.03 (0.02)	0.17 (0.06)	0.11 (0.04)	0.30 (0.07)	11.5	0.01
Aspidosperma	0.01 (0.01)	0.05 (0.02)	0.03 (0.02)	0.02 (0.01)	4.4	0.22
Astronium urundueva	0.00	0.01 (0.01)	0.01 (0.01)	0.05 (0.02)	14.9	<0.001
Caesalpinia pluviosa	0.01 (0.01)	0.03 (0.02)	0.05 (0.02)	0.04 (0.02)	5.5	0.14
Centrolobium microchaete	0.01 (0.01)	0.03 (0.02)	0.04 (0.02)	0.02 (0.01)	0.7	0.88
Copaifera chodatiana	0.02 (0.02)	0.13 (0.04)	0.06 (0.02)	0.04 (0.01)	10.0	0.02
Acosmium cardenasii	0.12 (0.03)	0.47 (0.12)	0.29 (0.08)	0.10 (0.06)	13.4	0.004

Note: Twelve commercial tree species were recorded in treated gaps, but only those species with densities greater than 0.01/m^2 are reported. Kruskal–Wallis nonparametric tests were used to test for differences among treatments. Standard errors are in parentheses (n = 12).

Fig. 1. Average density (per square metre) of commercial trees (seedlings and sprouts) regenerating in felling gaps 6 years after high-intensity burns, low-intensity burns, and mechanical cleaning. Height size-classes are indicated on the x-axis: 1, 0–10 cm; 2, >10–30 cm; 3, >30–150 cm; 4, >150 cm. (Results of Kruskal–Wallis nonparametric tests comparing these size classes among treatments are as follows: 1: χ^2 = 2.3, p = 0.51; 2: χ^2 = 1.6, p = 0.66; 3: χ^2 = 15.1, p < 0.001; 4: χ^2 = 16.6, p < 0.001.)

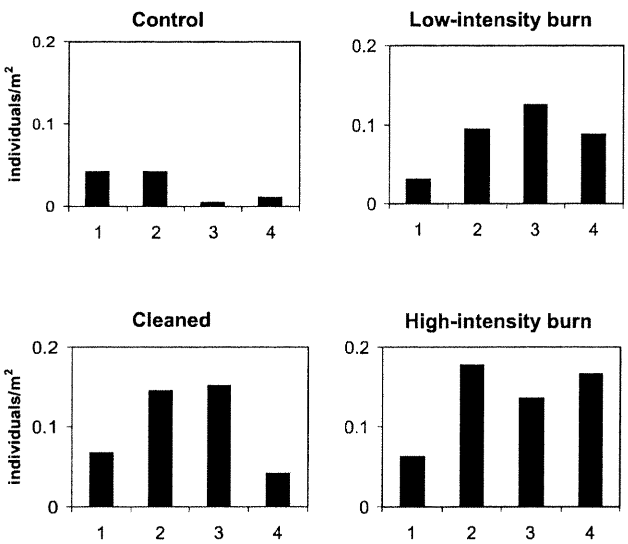
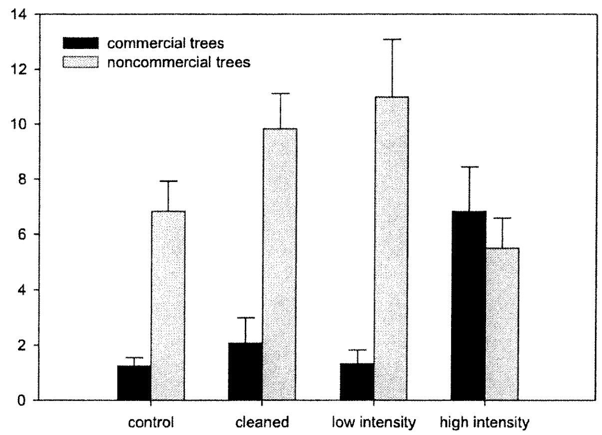


Fig. 2. Density of commercial and noncommercial trees >2.5 m tall in 100-m^2 treatment plots 6 years after high-intensity burns, low-intensity burns, and mechanical cleaning (bars represent SE; n = 12).



8-m resprout found in a high-intensity burn plot. This species also dominated the commercial tree regeneration in the other treatments, accounting for 66% of commercial trees >2.5 m tall in the control, cleaned, and low-intensity burn plots. Except for one individual in a cleaned treatment, all regeneration of *Astronium urundueva* >2.5 m tall was in high-intensity burn plots.

Competing vegetation

Total vegetation cover (both <2 m and >2 m) was similar among the four treatments 6 years after prescribed burns (Fig. 3). There was no difference in tree or liana cover among treatments (both <2 m and >2 m). Percent cover of the ground bromeliad, *Pseudananas sagenarius*, was significantly greater in control plots than in other treatments (χ^2 = 30.1, p < 0.0001). Herb cover was greater in high-intensity burn plots than in other treatments (χ^2 = 9.2, p < 0.03). Shrub cover also differed among treatments (χ^2 = 10.2, p < 0.02), although its total range was only 3%–6%.

Density of noncommercial trees >2.5 m tall was four to six times greater than that of commercial trees in the control, cleaned, and low-intensity burn treatments (Fig. 2). Only in the high-intensity burn treatment was the density of noncommercial trees >2.5 m tall less than that of commercial trees. In fact, density of noncommercial trees >2.5 m tall in high-intensity burn plots was half that in low-intensity burn plots (F = 3.1, p = 0.04). The most common noncommercial tree >2.5 m tall was *Casearia gossyiosperma*, an understory tree that regenerated primarily from stem sprouts. The second most common was *Acacia lorentensis*, a shade-intolerant canopy tree that regenerated from a combination of seedlings and sprouts. Regeneration of *Acosmium cardenasii*, a noncommercial species, but the most abundant canopy tree in this forest, differed among treatments. Densities of this species, both individuals >2.5 m tall (Table 3) and individuals of all sizes (Table 2), were highest in the cleaned treatment.

Soil cations and organic matter

Ca and K concentrations and cation exchange capacity were significantly higher in the high-intensity burn treatment

Table 3. Species with individuals >2.5 m tall 6 years after site-preparation treatments in a Bolivian dry forest.

Species	Total no.	Height (m)	Percentage of total in treatments (%)			
			Control	Cleaned	Low intensity	High intensity
Commercial species						
Centrolobium microchaete (C. Martius ex Benth.) H.C. de Lima	64	4.8	19	28	11	42
Anadenanthera colubrina (Vell. Brenan)	43	3.5	0	9	12	79
Astronium urundueva (Allemao) Engl.	14	3.2	0	8	0	92
Tabebuia impetiginosa (Mart. Ex DC.)	10	3.6	10	10	10	70
Caesalpinia floribunda Tul.	5	3.4	0	20	60	20
Cordia alliodora	2	3.0	0	50	50	0
Noncommercial species						
Casearia gossypiosperma Briq.	91	3.0	9	32	38	21
Acacia loretensis J.F. Macbr.	75	4.5	19	41	29	11
Casaeria arborea (Rich.)	47	3.2	23	17	40	19
Neea hermaphrodita S. Moore	38	3.0	24	39	32	5
Acosmium cardenasii H. S. Irwin & Arroyo	26	4.2	12	54	27	8
Spondias mombin L.	14	3.1	7	7	57	29
Luea paniculata Martius	12	4.1	25	0	42	33
Galipea trifoliata Aubl.	10	2.5	30	30	30	10
Urera baccifera (L.)	10	3.9	40	30	10	20
Eriotheca roseorum (Cuatrec.)	10	4.3	30	20	30	20
Simira rubescens (Benth.) Bremek ex Steryerm	8	3.9	38	13	50	0
Sauco	7	3.4	14	43	29	14
Chorisia speciosa St. Hilaire	7	3.2	57	0	14	29
Gallesia integrifolia	6	4.1	0	33	0	67
Gossypiospermum	4	4.5	25	25	25	25
Bougainvillea modesta Heimerl	4	4.1	25	0	50	25
Cecropia concolor Willd.	3	4.7	33	0	0	67
Limoncillo	3	3.8	33	0	67	0
Moradillo	3	3.2	100	0	0	0
Combretum leprosum Mart.	2	5.8	50	50	0	0

than in the other treatments 6 years after burns ($F = 15.4$, $p < 0.001$; $F = 3.3$, $p = 0.028$; $F = 13.9$, $p < 0.001$, respectively). Concentrations of Mg and organic matter content were not significantly different among treatments. Soils in high-intensity burn treatments also had a higher clay fraction than did soils in other treatments ($F = 9.2$, $p < 0.001$). However, the fractions of silt and sand did not differ among treatments.

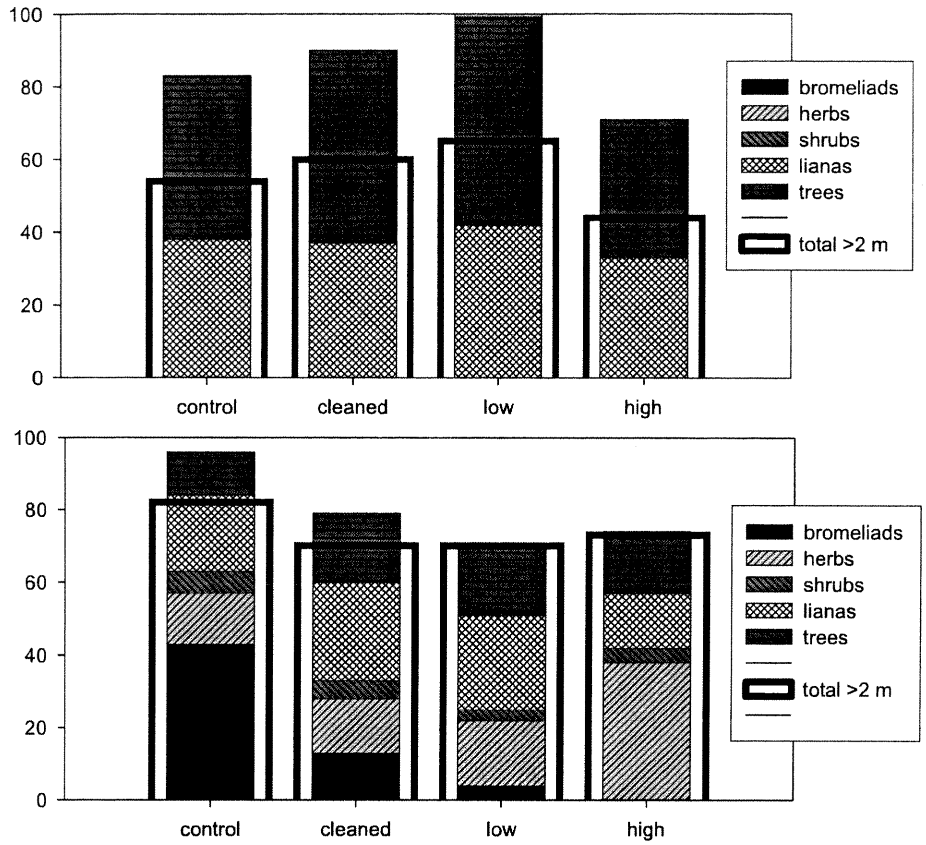
Discussion

High-intensity burns enhanced the regeneration of commercial tree species, particularly the shade-intolerant species regenerating from seed (*Anadenathera colubrina* and *Astronium urundueva*). These species were both more abundant and taller in the high-intensity burn treatment than in other treatments. These findings confirm trends that were beginning to appear during the first 18 months after burns, but were not significant (Kennard and Putz, in press). Furthermore, commercial species as a group tended to dominate regenerating vegetation in high-intensity burn treatments. While commercial trees >2.5 m tall were found in the other three treatments, noncommercial tree species or vines usually overtopped them. This vigorous regeneration of competing vegetation may prevent longer term success of commercial tree regeneration in treatments where tree density was moderate (low-intensity burn and cleaned treatments).

The one exception to this pattern is *C. microchaete*. Root sprouts of this species tended to be taller than the regeneration of both commercial and noncommercial species alike, regardless of treatment. The regeneration strategy of *C. microchaete* contributes to its high growth rates. Earlier measurements confirmed that while sprouts of all species generally had higher growth rates than did seedlings (Kennard et al. 2002), *C. microchaete* sprouts grew more rapidly than sprouts of other species. This is likely because they sprout from the root systems of mature trees and therefore have larger carbohydrate reserves to use than do sprouts of other species in this forest, which mostly originate from juveniles.

The success of shade-intolerant commercial species in the high-intensity burn treatment is likely the result, in part, of decreased competition during the first 6 years of the study. During the first 18 months following burns (a critical period for seedling establishment and survival), total vegetation cover was lower in the high-intensity burn plots than in the other treatments (Kennard et al. 2002). Also, the dominant individuals were most frequently commercial trees or herbs in high-intensity burn plots. In contrast, noncommercial trees and vines dominated the other treatments. These lower levels of competing vegetation in high-intensity burn plots persisted through the first 6 years. In 2003, there were still fewer tall (>2.5 m) noncommercial trees in high-intensity

Fig. 3. Total vegetation cover (solid line) and percent cover by life form (>2 m and <2 m height) in felling gaps 6 years after high-intensity burns, low-intensity burns, and mechanical cleaning. Where cover of different life forms overlapped, their sum will be greater than total cover (total cover cannot exceed 100%). No bromeliads, herbs, or shrubs were found taller than 2 m (top graph).



burn plots than in any other treatment. And although total vegetation cover had converged among treatments by 6 years, more of this cover was composed of herbaceous vegetation in high-intensity burn plots. Herbaceous vegetation rarely reaches heights >1.5 m and therefore is unlikely to compete with taller commercial trees for light.

The other possible explanation for the success of shade-intolerant commercial species in the high-intensity burn treatment is the pulse of soil nutrients caused by the fire. Immediately following controlled burns, surface soils in high-intensity burn treatments had higher concentrations of extractable Ca, K, Mg, and P and higher amounts of resin-available P and N (Kennard and Gholz 2001). Although this effect was likely important only during the first year following burns (by 18 months, increased levels of K and Mg and resin-available P and N were no longer significant), this time period is crucial for establishing seedlings, because it helps to determine their ability to compete in later years (Brokaw 1985; Uhl et al. 1988).

It was expected that recently established seedlings in high-intensity burn plots would show the effects of degraded soil structure. Loss of soil organic matter during high-intensity fires contributed to increased bulk density and strength and to decreased water infiltration rates during the first 18 months (Kennard and Gholz 2001). However, this expectation was not met. The density of commercial species that likely established after the first 18 months (conservatively, seedlings >30 cm tall at the 6-year remeasurement) was not lower in the high-intensity burn plots than it was in other treatments (Fig. 1). Nevertheless, the fact that altered soil texture was still evident 6 years after high-intensity burns confirms that intense, hot fires can degrade the structure of these soils. Moreover, intense fires are more likely to lead to erosion problems, since the entire forest floor is consumed during these burns.

While high-intensity burns increased the regeneration success of commercial species as a whole, it did not have a positive effect on *Copaifera chodatiana*, *Aspidosperma rigidum*, or *Caesalpinia pluviosa*. These species are either shade tolerant (*Copaifera chodatiana*) or intermediate in their shade tolerance (*Aspidosperma rigidum* and *Caesalpinia pluviosa*) and did not exhibit high growth rates during the first 18 months following burns in any treatment (Kennard and Putz, in press). Moreover, all of these species had advance regeneration in the study plots before the site-preparation treatments were applied. These results highlight the inherent conflict between promoting regeneration of shade-intolerant species with intense silvicultural treatments while trying to maintain regeneration of shade-tolerant species. Where advance regeneration of shade-tolerant species is abundant, less intense treatments that release seedlings and saplings from competition (such as weeding or thinning) would be more suitable than prescribed burning.

The results of this study provide an interesting contrast to findings of similar studies conducted in this region of Bolivia. Heuberger et al. (2002) examined regeneration of commercial timber species following mechanical cleaning, prescribed burning, and a combination of both treatments and found no significant differences in overall density among treatments. Pinard et al. (1998) examined the same species following a combination of mechanical cleaning, burning, soil scarification, and gap-enlargement treatments and also found no differences in overall commercial species density. Both studies reported differences in growth rates of *Anadenathera colubrina* among treatments, but with different results. Heuberger et al. (2002) found *A. colubrina* to have the highest growth rates in the mechanical cleaning treatment and lowest growth rates in the burn-only treatment. In contrast, Pinard et al. (1998) found *A. colubrina* seedlings to be taller in burned than in unburned gaps. The seemingly inconsistent results between these two studies and the present one may be due to differences in fire intensity among the burning treatments. Fire intensity is an important determinant of the extent and duration of competition removal, the amount of mineral soil exposed, and increased nutrient availability. The high-intensity burn treatment in the present study, by design, was more intense than the burn treatments in the other two studies just discussed. While low-intensity burns controlled competing vegetation little more than mechanical cleaning did, high-intensity burns prevented regeneration of all but the most fire-tolerant sprouting species or those colonizing from dispersed seeds (Kennard et al. 2001).

This comparison suggests that shade-intolerant commercial species in this region require disturbances of rather high intensity in order to regenerate successfully. Also substantiating this pattern are the high densities of shade-intolerant commercial species found in slash-and-burn fallows of this region (Gould and Quiviquivi 2000; Kennard 2002). Local farmers time their burns to achieve intense fires that will minimize competition, remove slash from fields, and leave a nutrient-rich ash layer. Notably, farmers also continually weed their agricultural plots while growth is active. This suggests that continued competition control may also be necessary for successful regeneration of shade-intolerant timber species.

The lack of agreement among these three studies may also be due to the degree of variability in microsite conditions within treatments. Because the treatments in the studies by Heuberger et al. (2002) and Pinard et al. (1998) were designed to mimic management-scale operations, they were applied to gaps of irregular shape and size and fuels were not distributed evenly across the treatment gaps. The resulting heterogeneous burns likely reduced overall treatment effects, because of competing vegetation proliferating from unburned patches (Heuberger et al. 2002). Treatments of the present study were applied to uniformly enlarged gaps, fuels were distributed evenly over smaller areas, and prescribed burns were applied to achieve a consistent burn across treatment plots. While this created a sufficiently homogeneous treatment to detect enhanced regeneration, these experimental treatments were too labor intensive to be practical at a management scale. This comparison highlights the difficulties managers would face in obtaining uniform recruitment of commercial regeneration using management-scale prescribed burns.

The patterns found in the present study were likely more distinct as a result of the unusually high seed fall of both *Anadenathera colubrina* and *Astronium unrundueva* after the experimental burns were applied. Heuberger et al. (2002) noted that seed production of these species was unusually low in the year their burns were conducted, which reduced recruitment of these species in treated gaps. Because of irregular interannual seed reproduction, low seed longevity, and a patchy distribution of seed trees, seed limitation will be a problem for at least some commercial species in any given year (Heuberger et al. 2002). As fires of even low intensities kill buried seeds (Kennard et al. 2002), controlled burns should ideally be conducted before peak seed fall of targeted commercial species. However, in these seasonal forests, this period usually comes earlier in the dry season (Justiniano 1998), before forest-floor conditions are sufficiently dry to carry a fire. While manually redistributing collected seeds into burned areas would help solve this problem, it would also increase management costs.

Although this study indicates that fire can increase regeneration of shade-intolerant commercial species, success of the management-scale application of prescribed burning in this region of Bolivia remains unclear. Currently, burning treatments are costly compared to other silvicultural treatments used in Bolivia. The cost of treatments used in the Heuberger et al. study (2002) ranged between $25 and $55/ha. The burning treatments in particular were expensive because of the high labor costs involved with constructing firebreaks and monitoring fires. As some authors have suggested (e.g., Rice et al. 1997), present investments in silvicultural treatments for a tree crop that will be harvested in 30 years are unlikely to be financially attractive given the high discount rates typical of many tropical countries. Burning larger areas may be more cost effective, as cost per unit area decreases with increasing burn size. However, conducting large burns requires considerably more skill than conducting smaller burns, and training of burn crews can become more important and possibly more expensive. Also, fires are unlikely to carry in forest understories except during severe dry seasons when the risk of escapes is highest.

If controlled burning is adopted as a forest management tool in Bolivia, it should be included as part of a larger integrated fire management system that has the resources to actively manage all fire situations, including preventing, or suppressing, undesirable fires (Goldammer 1994). Wildfires resulting from escaped prescribed burns, and the carbon emissions that occur, can quickly offset any benefits derived from prescribed burns. During the dry season of 1999, for example, wildfires damaged over 3 million ha of forestland in the Department of Santa Cruz alone (Cordero 2000). The estimated carbon emissions from this single fire season, an estimated 17.3 million tons (1 ton = 907.174 74 kg) of carbon, are roughly equivalent to the 30-year carbon-offset goal of a 2.1-million-ha addition to the Noel Kempff Mercado National Park in eastern Bolivia (Environmental News Network 1998). In addition to the relevant ecological and economic knowledge, an integrated fire management system requires substantial infrastructure and trained personnel. Many Bolivian forest managers express doubt that fire management will be conducted in Bolivian forests in the near future, citing as two important barriers to implementation the inaccessibility of forests and the weak institutional capacity of organizations that might eventually conduct fire management (Gould and Quiviquivi 2000).

Conclusions

In the seasonally dry forests of Bolivia, shade-intolerant commercial species require intense disturbance for their regeneration. The results of this study suggest that by decreasing competing vegetation and increasing soil nutrients, high-intensity fire improves regeneration of these species. However, several ecological, economic, and social barriers currently preclude the management-scale application of prescribed fire in Bolivia: (*i*) Intense fires that are likely required for shade-intolerant tree regeneration are impractical on larger scales. Intense fires degrade soil structure and likely have other negative effects on forest structure and composition. (*ii*) Low-intensity or patchy fires do not provide sufficient competition control for shade-intolerant species. Management-scale burns would therefore have inconsistent regeneration. (*iii*) Fire of any intensity is not beneficial for commercial tree species with shade-intolerant or intermediate regeneration. (*iv*) Costs are currently too high to make prescribed burning a viable management tool. (*v*) Current infrastructure and institutional capacity in Bolivia may not support an integrated fire management system.

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