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Post-fire tree regeneration in lowland Bolivia: implications for fire management

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Abstract

Tree regeneration was compared in burned and unburned portions of a tropical dry forest (1110 mm ppt/year) and a tropical humid forest (1542 mm ppt/year) in southeastern Bolivia. Both forests burned 5 years prior to our study, and both forests were also lightly selectively logged (intensity < 1 m^3/ha)—the dry forest during the 1970 and 1980s and the humid forest just prior to the wildfire. The objective of this study was to compare abundance, size, and mode (seedling or resprout) of tree regeneration in burned and unburned areas of these forests, focusing on the most common canopy tree species and the commercial timber species at each site. Regeneration of 13 species of trees was quantified in the humid forest and 12 species in the dry forest. Tree regeneration <5 cm basal diameter but >20 cm tall was more abundant in the dry forest ($\bar{x}$ = 1807 stems/ha) than in the wet forest (x = 490 stems/ha). In both forests, resprouts were generally larger but less abundant than seedlings. In the dry forest, regeneration of the following commercial tree species was significantly more abundant in the burned areas: *Cedrela fissilis*, *Anadenanthera colubrina*, *Astronium urundueva*, and *Centrolobium microchaete*. However, *Acosmium cardenasii*, a canopy tree species not marketed for timber in Bolivia, represented the majority of regeneration (63%) in the dry forest and was equally abundant in burned and unburned areas (~1100 stems/ha). In the humid forest, only one timber species, *Aspidosperma rigidum*, was more abundant in burned than unburned areas (51 vs. 0 stems/ha, respectively). Another timber species that is rarely harvested in the region, *Pseudolmedia laevis*, was significantly less abundant in the burned than unburned area (22 vs. 173 stems/ha, respectively). The results of this study suggest that controlled burning could increase the abundance of timber tree regeneration at the dry forest site and to a lesser extent at the humid forest site. No data were collected to assess the likelihood that this increased density of regeneration will result in increased harvestable timber. However, local forest management institutions do not presently appear capable or motivated to conduct fire management—whether for enhancing timber regeneration or for limiting the damage caused by accidental wildfires.
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Keywords: Bolivia; Coppicing; Tropical dry forest; Cedrela; Fire; Tropical forestry; Regeneration; Resprout

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1. Introduction

Fire is an important but poorly understood force influencing the structure and composition of nearly all

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tropical forest ecosystems (e.g., Sanford et al., 1985; Bond and Wilgen, 1996). Increasing fire frequencies in tropical forests are causing dramatic changes in species composition, structure, and economic value of forests (Holdsworth and Uhl, 1997; Uhl, 1998; Mostacedo et al., in press; Cochrane and Schulze, 1999; Goldhammer, 1999). One important way that fires affect forests is by changing patterns of regeneration (Bond and Wilgen, 1996).

In tropical deciduous forests, coppicing (resprouting) is reportedly the primary response of woody species to disturbance (Murphy and Lugo, 1986; Hardesty et al., 1988; Kauffman, 1991; Miller and Kauffman, 1998), but seedling regeneration is also an important source of post-disturbance regeneration (Lieberman and Li, 1992; Swaine, 1992; Miller and Kauffman, 1998). In the studies of post-fire regeneration, resprouts tend to be larger than their seedling counterparts (Stocker, 1981; Kauffman, 1991), in part because resprouts can draw on carbohydrate reserves stored in their roots (Miller and Kauffman, 1998). In addition, resprouts may begin to grow as soon as site conditions are favorable, while seedlings are dispersal limited (Kauffman, 1991; Kennard, 2000). However, where fires destroy both above and below-ground biomass, seedling colonization is necessary.

Understanding the responses of different tree species to fire may permit use of controlled burns to enhance regeneration of valuable timber species (Smith, 1986). In the United States, for example, fire has been used to favor advance regeneration of fire-resistant oak seedlings over fire-sensitive regeneration of less valuable species (Johnson, 1993). In the broad-leaved forests of the tropics, there have been relatively few studies to assess the potential of controlled burning for improving timber regeneration. Notable exceptions are recent experimental investigations by Stanley (1999) and Kennard (2000) in lowland forests of Guatemala and Bolivia, respectively. Both authors found that prescribed burns can be used to enhance timber regeneration in logging gaps.

The present study enlarges upon the work of Mostacedo et al. (in press), who studied the effects of the same wildfires on forest structure and species richness. They found that fires caused greater structural damage in the sub-humid than the dry forest and that the effects of fire on species richness varied by forest strata. These authors also found that densities of saplings and shrubs (>2 m tall and <10 cm DBH) were consistently more abundant in the burned areas at both sites. This study enlarges upon Mostacedo et al.'s (in press) work by more closely examining the effects of the fires on the regeneration of the most common and economically important tree species in the dry and sub-humid forests. We compared the abundance, size, and mode (seedling or resprout) of canopy tree regeneration in burned and unburned sections of each forest. Based on the regeneration data we make some predictions about the response of timber regeneration to prescribed burns. Finally, we make a preliminary assessment of the status of fire management activities in the region based on interviews with professionals working in the forestry sector.

2. Methods

2.1. Study sites

Las Trancas is a seasonally dry tropical forest managed by the Chiquitano indigenous community in the Lomerio region, south of Concepción (16°13′S, 61°50′W). Mean daily temperature in the region is 24 °C and mean annual precipitation is about 1110 mm (CORDECRUZ/SENAMHI, 1994: meteorological data from Concepción). Most of Las Trancas is upland forest with the 14–18 m open-canopy stratum becoming mostly deciduous during 6–7 months dry season. The upland portions of the site are dominated by a few tree species, most numerous of which are *Anadenanthera colubrina* and *Acosmium cardenasii*. Very selective logging (<1 tree/ha/20 years) for *Machaerium scleroxylon*, *Cedrela fissilis*, and *Amburana cearensis*, was carried out at the site in the 1970s and 1980s (Bejarano, 1998). Fire frequency in Las Trancas is probably much higher today than it was in recent history because of the many fires that reach the forest edge from adjacent pastures and agricultural fields during the annual "burning season" (Pinard and Huffman, 1997; T. Killeen, pers. comm.).

La Chonta is a timber concession located within the Guarayos Forest Reserve (15°45′S, 62°60′W). The site is classified as a sub-humid tropical forest with a mean annual temperature of 24.5 °C and mean annual rainfall of approximately 1542 mm (CORDECRUZ/

SENAMHI, 1994: meteorological data from Ascensión de Guarayos). Some tree species are deciduous, but most retain their leaves during the 4-month dry season. The closed forest canopy averages 20–22 m tall and is dominated by tree species characteristic of humid forests in Bolivia, including *Hura crepitans*, *Ficus glabrata*, and *Pseudolmedia laevis* (Gil, 1998). Selective logging of mahogany (*Swietenia macrophylla*) had been carried out in the 2 years prior to the occurrence of wildfire on this site (logging intensity ca. 1 m^3/ha, J. Ledezma, pers. comm.).

Towards the end of the dry season of 1993 (Las Trancas) and 1994 (La Chonta), wildfires burned large areas of forest at both study sites. Both wildfires are thought to have originated from pasture fires set to rejuvenate forage for cattle. Although extensive areas of both sites were burned, the arrival of heavy rains extinguished fires leaving areas of unburned forest apparently similar in site characteristics and species composition to those areas affected by the fire. Since logging had been carried out prior to the fire in La Chonta, fuel loads were likely higher than at Las Trancas. In 1995, the 1-year post-fire responses of trees and vines to the fire at La Chonta were described by Pinard et al. (1999b).

2.2. Sampling design

Between June and August 1998, approximately 5 years after the fires, plant communities were sampled in burned and adjacent unburned areas at both sites. With the help of local guides who had witnessed the fires, sampling areas were chosen at both sites where the fire had passed with what they considered to be high intensity. The only apparent differences between burned and unburned plots was that rains had apparently extinguished the fires before they reached the control areas.

Within each forest, a principal transect was established running through the apparent center of the burned and unburned area. At 100 m intervals, secondary transects were established perpendicular to the primary transect. Sampling locations were then located at 50 m intervals along the secondary transects. At each sampling location, $9 \times 9\,m^2$ plots were established. These plots were used to sample 12 species of trees at Las Trancas and 13 species at La Chonta. Regeneration was quantified in 15–18 plots per treatment at each site. In the unburned forest at the La Chonta concession, all plots that fell within <2 year-old logging gaps were repositioned 25 m further down the transect. Such gaps were not present at the other sampling locations. The tree species that were sampled were chosen because of their abundance or because they produce valuable timber. Although regeneration of species other than those on our list were not quantified, the included species represent the majority of regeneration found in sites where data were collected. All seedlings or sprouts of the chosen species that were >20 cm tall of the target species and with basal diameter $\leq$5 cm were quantified. Furthermore, seedlings and resprouts <20 cm tall of the target species were counted and identified in two $1 \times 1\,m^2$ sub-plots located in the center of each $9 \times 9\,m^2$ plot.

We choose 5 cm as the maximum basal diameter because we believe that no tree species at either site could have grown larger than 5 cm in maximum basal diameter in the 5 years since the wildfires. In addition, few if any plants <5 cm basal diameter survived the fire (Pinard et al., 1999b). All individuals of the selected species found in the plots were identified, and their heights, canopy widths, and basal diameters were measured. The volume of each plant was estimated by multiplying stem height by the minimum and maximum canopy widths. Volume was used as a proxy for plant size instead of the more traditional stem diameter or height because stem-resprouts have basal stem diameters that are disproportionately large compared to their height, and because seedlings and resprouts tend to have different architectures. However, stem height and basal diameter are correlated with volume: $\text{volume} = 0.015 \times \text{height} - 0.72$, $R^2 = 0.482$, $F = 652$, $P < 0.0001$; $\text{volume} = 0.12 \times (\text{basal diameter}) - 0.56$, $R^2 = 0.395$, $F = 424$, $P = 0.0001$, $N = 652$.

Any plant that sprouted after being top-killed or that grew from a root rather than a seed was defined as a resprout. Basal scars on stems and root crowns helped us to distinguish resprouts from seedlings. Because we did not completely excavate apparent seedlings, we probably underestimated the frequency of resprouts.

2.3. Local fire management capacity

Nine leading professionals employed in the fields of forestry and conservation in Santa Cruz, Bolivia were interviewed. Each interviewee was asked his/her

opinion about institutions, policies, and practices related to fire management in the region.

2.4. Analysis

Because single large burned and unburned areas were compared at each site, the experimental design of this study involved pseudo-replication. Nevertheless, standard parametric and non-parametric tests were used to assess differences between burned and unburned plots, with the factors being burned vs. unburned and seedling vs. resprout. In addition, we compared the density and size of regeneration in burned and unburned areas for each species. We assumed Poisson distributions for the counts and tested for a difference between the means using SAS PROC GEN MOD, Version 7 (SAS Institute, Cary, NC). All other data analysis was conducted using JMP 3.12 (SAS Institute, Cary, NC). Due to the large number of statistical tests performed in this investigation, differences were considered statistically significant at the 0.01 level unless otherwise indicated.

3. Results

3.1. Abundance of seedlings and resprouts in burned and unburned plots

The dry forest site had almost four times as much regeneration as the humid forest site: dry forest ($\bar{x} \pm$ S.E.): 1807 ± 223 stems/ha, humid forest: 490 ± 63 stems/ha. At the dry forest, the burned areas (2209 ± 247 stems/ha) had more regeneration than the unburned areas (1404 ± 354 stems/ha, $t = 1.86$, $P = 0.07$), while at the humid forest, there was no difference between the number of regenerating stems in burned (449 ± 82 stems/ha) and unburned areas (536 ± 100 stems/ha, $t = 0.66$, $P = 0.51$). Seedlings were five to eight times more abundant than resprouts except in the burned part of the humid forest where seedlings were only twice as abundant as resprouts (Table 1).

Seedlings <20 cm tall of the focal species were between 20 and 40 times more abundant in the dry forest ($\bar{x} = 20{,}400 \pm 4700$ stems/ha, $N = 148$) than in the humid forest ($\bar{x} = 700 \pm 400$ stems/ha, $N = 5$). In addition, within each site, small seedling densities were not greater in burned than unburned forest ($t = 1.7$, $P > 0.05$).

3.2. Size of seedlings and resprouts in burned and unburned plots

Resprouts tended to have greater median volume than seedlings in burned and unburned plots (Table 2). In addition, regeneration in burned plots tended to be larger than regeneration in unburned plots (Table 2). Furthermore, in burned areas of both sites, the probability of a given stem being a resprout increased with the size of the regenerating stem (Pearson's chi-square test: $\chi^2 = 49.6$, $P < 0.0001$; Fig. 1a). This trend was not apparent in unburned areas (Pearson's chi-square test: $\chi^2 = 9.6$, $P = 0.38$; Fig. 1b).

3.3. Abundance and size of regeneration of individual species

At both sites, a few tree species produced the majority of the regeneration. In the humid forest,

Table 1
Abundance of regeneration in a burned and an unburned tropical dry and tropical humid forests in SE Bolivia

Site	Regeneration class	Burned forest			Unburned forest		
		N	x[a] (stems/ha)	S.E.	N	x (stems/ha)	S.E.
Dry forest	Seedling	286	1962 a	235	169	1165 b	327
	Resprout	36	247 c	47	38	239 c	70
Humid forest	Seedling	43	312 xy	64	58	478 x	86
	Resprout	19	137 yz	26	7	58 z	23

[a] Within each site, treatment effects of regeneration class and burned vs. unburned forest were detected using an ANOVA. Means were separated using a Tukey–Kramer HSD multiple comparisons procedure with $P \leq 0.05$. Means within each site followed by different letters are significantly different. Seedlings and resprouts are >20 cm tall and have basal diameters ≤5 cm.

Table 2
Size of regeneration in a burned and an unburned tropical dry and tropical humid forests in SE Bolivia

Site	Regeneration class	Burned forest		Unburned forest	
		N	Median volume per stem (m^3)[a]	*N*	Median volume per stem (m^3)
Dry forest	Seedling	286	0.018 a	169	0.014 a
	Resprout	36	0.928 b	38	0.018 a
Humid forest	Seedling	43	0.288 x	58	0.043 y
	Resprout	19	0.714 x	7	0.112 xy

[a] Within each site, treatment effects of regeneration class and burned vs. unburned forest were detected using the Kruskal–Wallis rank sums test. Sizes were compared using Mann–Whitney test with $P \leq 0.01$ to account for multiple comparisons. Medians within each site followed by different letters are significantly different. Seedlings and resprouts are >20 cm tall and have basal diameters ≤5 cm. Volume per individual in m^3 was estimated by multiplying the maximum canopy width by the minimum width by the stem height.

the four most common species accounted for 86% of the regeneration (Table 3). In the dry forest the regeneration was dominated by *A. cardenasii* (63% of the total). Seven other species in the dry forest each accounted for between 3 and 8% of the remaining regeneration (Table 3). Similarly, at each site, only a few species of trees produced the majority of regenerating stems ≤20 cm tall. At the dry forest site, the smallest size class of regeneration was dominated by *A. colubrina* (75%) and *A. cardenasii* (18%). Both species were equally abundant in burned and unburned areas. In the humid forest only five regenerating stems ≤20 cm tall were found in the 36 plots (four individuals of *H. crepitans*, and one individual of *Aspidosperma rigidum*).

Post-fire regeneration was enhanced for some species and reduced for others (Table 3). In the dry forest, regeneration of *C. fissilis*, *A. colubrina*, *Centrolobium microchaete*, and *Astronium urundeuva* were significantly more abundant in burned than unburned areas (difference between Poisson means, $P < 0.01$, Table 3). In contrast, *A. cardenasii*, the most common species, was found with equal frequency in both areas ($t = 0.3, P = 0.77$). In the humid forest, *A. rigidum* was more abundant in burned areas, while *P. laevis* was significantly more abundant in unburned areas (difference between Poisson means, $P < 0.01$, Table 3).

The general trend for seedlings to be more abundant, but smaller than resprouts (Tables 1 and 2), was usually consistent when the species were analyzed separately (Tables 3 and 4). *C. fissilis* and *H. crepitans* were represented solely by seedlings. In contrast, the pattern of larger regeneration in burned areas was not consistent when the species were analyzed separately (Table 4).

C. fissilis and *C. microchaete* both increased in abundance following fire but via contrasting regeneration strategies. *C. fissilis* regenerated exclusively from seed, while *C. microchaete* regenerated more commonly from resprouts (Table 3). Approximately, half of the *C. microchaete* regeneration was of resprout origin, but the correct figure is likely much higher; *C. microchaete* resprouts from deep roots so stem bases of seedlings and resprouts are equally free of scars and are therefore difficult to distinguish.

3.4. Results of interviews

All individuals interviewed agreed that in southeastern Bolivia neither controlled burning to promote regeneration of commercial species nor fire management to prevent wildfires is currently being carried out. However, ranchers use fire to maintain their pastures and small-scale farmers use fire to prepare their lands for planting. There was also agreement that fires that escape from ranchers and farmers have caused many of the wildfires that have occurred in recent years. "Vandalism" was also cited as an important cause of wildfire. The interviewees expressed little confidence that existing institutions have either the capacity or the incentive to control wildfires on forest lands. Institutions that interviewees were asked to consider include local, municipal, and federal government agencies, non-government organizations, concessionaires, private land owners, and indigenous groups. Furthermore, no one was aware of any quantitative studies

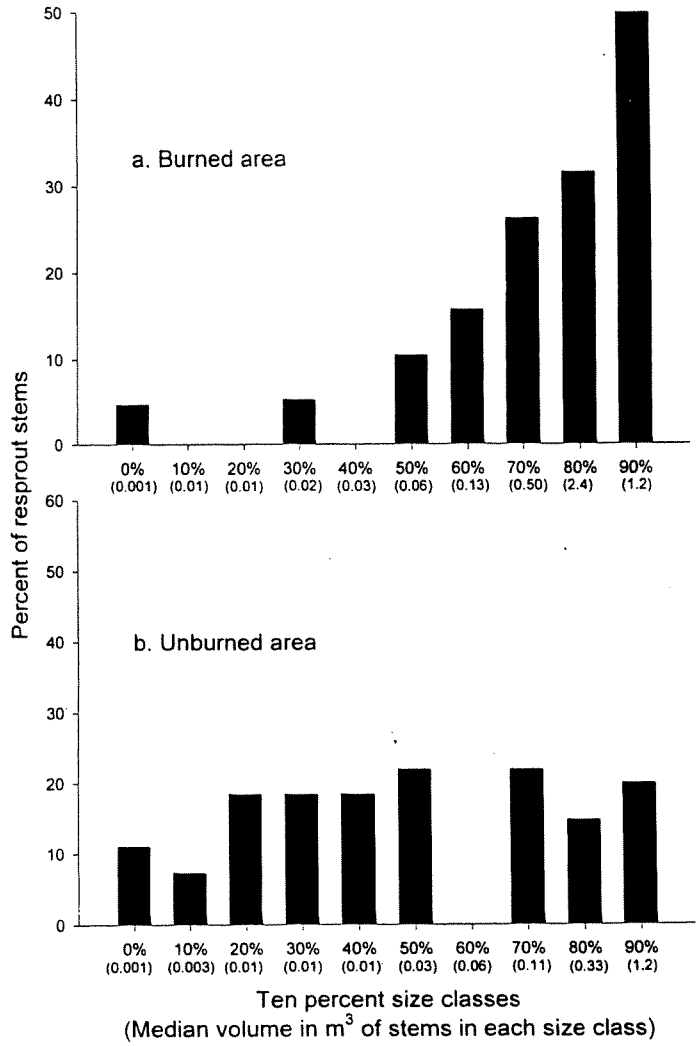

Fig. 1. The percent of stems of resprout origin are shown for each 10% size class. Volume per stem in m^3 was estimated by multiplying the maximum canopy width by the minimum width by the stem height. Data from the wet and humid forest sites were combined because the same trends were apparent for both sites. (a) Pearson's chi-square test: $\chi^2 = 49.6, P < 0.0001, N = 384$ stems; (b) Pearson's chi-square test: $\chi^2 = 9.6, P = 0.38, N = 268$ stems.

describing the economic costs of wildfires in the region. Finally, there was general agreement that controlling wildfires will be extremely difficult because the forests of the region are vast and relatively inaccessible.

4. Discussion

We found contrasting patterns of post-fire regeneration in the dry and humid forests in this study. Wildfire appears to have stimulated tree regeneration in the dry forest, but had little effect in the humid forest. These findings corroborate Mostacedo et al.'s (in press) hypothesis that the dry forest, which is more prone to fire, also has more species that are better adapted to fire than does the humid forest. The majority of the timber species at Las Trancas had enhanced regeneration in burned areas. The regeneration of non-commercial tree species, in contrast, was not enhanced by fire. These results corroborate

Table 3
Abundance of seedling and resprout regeneration in a burned and an unburned tropical dry and tropical humid forests in SE Bolivia[a]

	Number of regenerating stems[b]		99% confidence interval for the ratio of estimated abundances of regeneration in burned vs. unburned forest[c]		Percent of regenerating stems that are resprouts		99% confidence interval for difference of proportions of resprouts in burned vs. unburned forest[d]		Regeneration niche[e]	Timber value[f]
	Burned forest	Unburned forest	Lower bound	Upper bound	Burned forest	Unburned forest	Lower bound	Upper bound		
Dry forest										
A. cardenasii	173	158	0.83	1.47	0.05	0.15	−0.19	−0.02	PST	N
A. colubrina (Vell. Conc.) Benth.	19	1	1.33	268.34	0.05	1.00	Insufficient data		SI	L
A. rigidum Rusby	17	8	0.70	6.41	0.18	0.13	−0.33	0.44	PST	L
Caesalpinia pluviosa DC.	20	8	0.85	7.40	0.20	0.38	−0.67	0.32	PST	L
C. fissilis Vell.	27	0	No regeneration in unburned forest		0.0	–	No resprout regeneration		SI	H
C. microchaete (C. Martius ex Benth.) Lima	30	0	No regeneration in unburned forest		0.5	–	No resprout regeneration in unburned forest		SI	H
Chorisia speciosa A. St. Hil.	3	11	0.06	1.61	0.0	0.18	−0.48	0.12	SI	N
Copaifera chodatiana	24	21	0.57	2.8	0.21	0.33	−0.47	0.22	PST	H
Humid forest										
A. rigidum	7	0	No regeneration in unburned forest		0.71	0.0	No resprout regeneration in unburned forest		PST	L
H. crepitans L.	9	11	0.41	4.17	0.0	0.0	0.00	0.00	SI	H
Inga sp. Miller	25	15	0.76	4.18	0.24	0.13	−0.21	0.42	PST	L
P. laevis (Ruiz and Pavón) J.F. Macbr.	3	21	0.03	0.62	0.67	0.10	−0.15	1.29	PST	L
Sorocea steinbachii C.C. Berg	8	17	0.17	1.53	0.63	0.18	−0.05	0.95	PST	N

[a] Five species at the dry forest site and seven species at the humid forest site were also quantified but were not included in the table because their regeneration was so scarce (less than 2% of individuals sampled). Dry forest: *Astronium urundueva* (Allemao) Engl., *Cecropia concolor* Willd, *Aspidosperma cylindrocarpon* Muell. Arg., *M. scleroxylon* Tul., and *Tabebuia impetiginosa* (C. Martius ex DC.) Standley. Humid forest: *C. speciosa*, *T. impetiginosa*, *Schizolobium amazonicum* Huber ex Ducke, *Chlorophora tinctoria* (L.) D. Don ex Steudel, *C. pluviosa*, *Ficus glabra* Vell., and *Spondias mombin* L.

[b] Sums of regenerating stems shown for the dry forest are from eighteen $9 \times 9\,m^2$ plots in burned forest and the same number of plots in unburned forest. In the humid forest there were 17 plots in the burned forest and 15 in the unburned forest.

[c] The upper and lower bounds shown correspond to a 99% confidence interval of the ratio between the abundance of regeneration in the burned vs. the unburned forest. In the case of *Acosmium*, for example, we estimate that the abundance of regeneration is 0.83–1.47 times greater in burned forest than in unburned forest. Since this interval contains 1, we cannot reject the null hypothesis that the abundance of regeneration is equal in the burned and unburned forests.

[d] The upper and lower bounds shown correspond to a 99% confidence interval for the difference between the proportion of resprouts to total regeneration in burned vs. unburned forests. In the case of *Acosmium*, for example, we estimate that the proportion of resprouts in burned forest is between 2 and 19% less the proportion of resprouts in unburned forests. Where the confidence interval includes 0, there is no evidence to reject the null hypothesis that the proportion of resprouts is equal in burned and unburned forests.

[e] Codes for regeneration niche—SI: shade intolerant; PST: partially shade tolerant (Pinard et al., 1999a; Lidezama, pers. comm.).

[f] Codes for timber value—H: high; L: low; N: none (Pinard et al., 1999b; Justiniano, pers. comm.).

Table 4
Size of regeneration in a burned and an unburned tropical dry and tropical humid forests in SE Bolivia[a]

	Median size[b] of regenerating stems in m^3							
	Burned forest				Unburned forest			
	Seedlings		Resprouts		Seedlings		Resprouts	
	N	Median[c]	*N*	Median	*N*	Median	*N*	Median
Dry forest								
A. cardenasii	165	0.014 a	8	0.285 b	133	0.012 a	22	0.014 a
A. colubrina	18	0.02 a	1	2.75 a	1	0.01 a	0	–
A. rigidum	14	0.005 a	3	0.245 b	7	0.26 b	1	0.33 ab
C. pluviosa	5	0.011 a	3	0.005 a	16	0.071 a	4	0.988 a
C. fissilis	27	0.064	0	–	0	–	0	–
C. microchaete	15	2.4 a	13	1.68 a	0	–	0	–
C. speciosa	3	0.089 a	0	–	9	0.063 a	1	0.028 a
C. chodatiana	19	0.01 a	5	0.12 b	14	0.06 ab	5	0.09 ab
Humid forest								
A. rigidum	2	0.309 a	5	1.4 a	0	–	0	–
H. crepitans	9	0.245 a	0	–	11	0.024 b	0	–
Inga sp.	19	0.683 a	6	0.318 a	13	0.057 a	2	0.119 a
P. laevis	1	0.12 a	2	1.00 a	19	0.038 a	2	0.024 a
S. steinbachii	3	0.047 a	5	0.275 a	14	0.092 a	3	0.371 a

[a] Five species at the dry forest site and seven species at the humid forest site were also quantified but were not included in the table because their regeneration was so scarce (less than 2% of individuals sampled). Dry forest: *A. urundueva*, *C. concolor*, *A. cylindrocarpon*, *M. scleroxylon*, and *T. impetiginosa*. Humid forest: *C. speciosa*, *T. impetiginosa*, *S. amazonicum*, *C. tinctoria*, *C. pluviosa*, *F. glabrata*, and *S. mombin*.

[b] Volume per individual in m^3 was estimated by multiplying the maximum canopy width by the minimum width by the stem height.

[c] Within each site, treatment effects of regeneration class and burned vs. unburned forest were detected using the Kruskal–Wallis rank sums test. Medians were separated using Mann–Whitney test with $P \leq 0.01$ to account for multiple comparisons. Medians within a row followed by different letters are significantly different.

Kennard's (2000) conclusion that controlled burns increase the abundance of regeneration of economically important species in this dry tropical forest. Despite this finding, we do not claim wildfires increase the economic value of the dry forest because wildfires damage and destroy much mature timber (Mostacedo et al., in press) and stimulate vine proliferation (Pinard et al., 1999b).

From a silvicultural perspective, it is important to consider both the quantity and quality of fire-induced tree regeneration. For example, relative to trees of seedling origin, resprouts are especially prone to buttrot which lowers timber quality (Hepting and Hedgecock, 1937) and makes trees more susceptible to fire damage. However, since *C. microchaete* tends to regenerate from root suckers, its timber may not suffer from the buttrot that is probably more characteristic of trees that sprout from broken or burned stem bases. However, more research is needed to assess the quality of the timber produced by post-fire, resprout regeneration of *C. microchaete* and *A. rigidum*. In contrast, *C. fissilis* regeneration in burned areas of the dry forest site may be of greater commercial value because all stems were of seedling origin.

The higher proportion of resprouts in the larger size classes of post-burn regeneration suggests that resprouts have greater survivorship compared to seedlings following wildfire (Fig. 1a and b). Miller and Kauffman (1998) found the same trend in regenerating agricultural fields in Mexico. Unless resprout regeneration experiences high mortality later in its development, our results indicate that post-fire forest composition will include a large proportion of trees of resprout origin.

Despite the promising patterns of post-fire tree regeneration in dry forests, these results must still be

considered tentative due to the brevity of this study. The regeneration we observed may not survive to produce harvestable timber if, as local farmers say, regenerating trees in burned areas ultimately become covered by vines. In addition, various authors have shown that increasing fire frequency can transform tropical forests into scrub (Goldhammer, 1999; Cochrane and Schulze, 1999; Menaut et al., 1995). If recent wildfires in SE Bolivia are the beginning of such a process, then the enhanced post-fire timber regeneration will not reach maturity.

Undoubtedly, more research could reveal appropriate controlled burning techniques for stimulating the regeneration of economically important species. However, it is also worthwhile to consider the probability that fire will be used to manage timber in the region in the short to medium term. We interviewed forestry professionals working in SE Bolivia, and all of them doubted that fire management would be conducted in Bolivian forests in the near future. According to the interviewees, the two primary barriers to implementing fire management are the inaccessibility of the forests and the absence of institutions with the interest or capacity to conduct fire management. In addition, controlled burning to enhance regeneration is an investment in future harvests of tropical timber, and many forest economists contend that such investments are economically unattractive, especially in less industrialized countries where discount rates are high (e.g., Rice et al., 1997). Thus, it appears that institutional and economic constraints will prevent the rapid adoption of controlled burning by forest managers in southeastern Bolivia.

Although fire may not be used to enhance timber regeneration in southeastern Bolivia in the near term, there is a critical need for fire management if accidental wildfires are to be controlled. Perhaps in part because of a lack of information, Bolivian policy makers are apparently ignoring wildfires. However, there is anecdotal evidence to suggest that wildfires cause considerable damage in the region. Pinard et al. (1999b) described a wildfire that burned over 1 million hectares of forest in the region in 1994. Although this fire burned thousands of hectares of the La Chonta forest concession, the concessionaire committed no personal or equipment to fighting the fire. In addition, during August 1999, wildfires burned over 1.6 million hectares in the Department of Santa Cruz including parts of five small towns and a municipal capital (Cordero, 2000). Notably, some forestry concessions and towns were protected from wildfires when bulldozers were used to create firebreaks (T.S. Fredericksen, pers. obs.).

5. Conclusion

Although fire is probably an integral component of ecological dynamics in southeastern Bolivia, the frequency of recent fires probably far exceeds the natural fire regime (Pinard and Huffman, 1997). Remote sensing technologies may enhance fire management capacity (Eva and Lambin, 1998) and thoughtful recommendations can help local institutions to get organized (ITTO, 1997). However, this research indicates that there are some formidable obstacles that must be overcome if fire is ever to be controlled or used for enhancing timber regeneration in lowland Bolivian forests.

This investigation focuses on the direct effects of wildfire (regeneration) and direct responses to wildfire (fire management). Although direct effects of and responses to wildfire are important to consider, we recommend that investigators place greater emphasis on identifying the underlying causes of the changes in fire frequency. Specifically, we suggest the following questions as starting points for future research. At the regional, national, and international levels: (1) what are the historical, social, and political factors that have changed fire frequency in SE Bolivia? (2) who stands to gain and to lose as a result of these changes?

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References

Bejarano, J., 1998. Plan de Manejo—Lomerio. Superintendencia Forestal, Santa Cruz, Bolivia.

Bond, W.J., Wilgen, B.W., 1996. Fire and Plants: Population and Community Biology Series 14. Chapman & Hall, New York, 263 pp.

Cochrane, M.A., Schulze, M.D., 1999. Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. Biotropica 31, 2–16.

CORDECRUZ/SENAMHI, 1994. Compendio Meteorologico del Departamento de Santa Cruz. Santa Cruz, Bolivia.

Cordero, W., 2000. Determinación del daño causado por los incendios forestales ocurridos en los Departamentos de Santa Cruz–Beni en los meses de agosto y septiembre de 1999. Final Report. Corporación Andina de Fomento, Proyecto BOLFOR, and Geosystems, Santa Cruz, Bolivia, 43 pp.

Eva, H., Lambin, E.F., 1998. Remote sensing of biomass burning in tropical regions: sampling issues and multisensor approach. Remote Sens. Environ. 64, 292–315.

Gil, P., 1998. Plan general de manejo forestal de empresa agroindustrial La Chonta Ltda. Superintendencia Forestal, Santa Cruz, Bolivia.

Goldhammer, J.G., 1999. Forests on fire. Science 284, 1782–1783.

Hardesty, L.H., Box, T.W., Malechek, J.C., 1988. Season of cutting affects biomass production by coppicing browse species of the Brazilian caatinga. J. Range Manage. 41, 477–480.

Hepting, G.H., Hedgecock, G.G., 1937. Decay in merchantable oak, yellow poplar, and basswood in the Appalachian region. US Dep. Agric. Tech. Bull. No. 570.

Holdsworth, A.R., Uhl, C., 1997. Fire in Amazonian selectively logged rain forest and the potential for fire reduction. Ecol. Appl. 7, 713–725.

ITTO (International Tropical Timber Organization), 1997. ITTO Guidelines on fire management in tropical forests. ITTO Policy Development Series No. 6.

Johnson, P.S., 1993. Perspectives on the ecology and silviculture of oak dominated forests in the Central and Eastern United States. General Technical Report NC-153. Unites States Department of Agriculture.

Kauffman, J.B., 1991. Survival by sprouting following fire in tropical forests of the Eastern Amazon. Biotropica 23, 219–224.

Kennard, D., 2000. Regeneration of commercial tree species following controlled burns in tropical dry forests in eastern Bolivia. Ph.D. Dissertation. University of Florida, Gainesville, FL.

Lieberman, D., Li, M., 1992. Seedling recruitment patterns in a tropical dry forest in Ghana. J. Veg. Sci. 3, 375–382.

Menaut, J.C., Lepage, M., Abbadie, L., 1995. Savannas, woodlands, and dry forests in Africa. In: Bullock, S.H., Mooney, H.A., Medina, E. (Eds.), Seasonally Dry Tropical Forests. Cambridge University Press, New York, pp. 64–92.

Miller, P.M., Kauffman, J.B., 1998. Seedling and sprout response to slash-and-burn agriculture in a tropical deciduous forest. Biotropica 30, 538–546.

Mostacedo, B., Fredericksen, T.S., Gould, K.A., Toledo, M., in press. Responses of community structure and composition to wildfire in dry and sub-humid tropical forests in Bolivia. J. Trop. For. Sci.

Murphy, P.G., Lugo, A.E., 1986. Ecology of tropical dry forest. Annu. Rev. Ecology and Systematics 17, 67–88.

Pinard, A.M., Huffman, J., 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. J. Trop. Ecol. 13, 727–740.

Pinard, M.A., Putz, F.E., Rumiz, D., Guzman, R., Jardim, A., 1999a. Ecological characterization of tree species for guiding forest management decisions in seasonally dry forests in Lomerio, Bolivia. For. Ecol. Manage. 113, 201–213.

Piñard, M.A., Putz, F.E., Licona, J.C., 1999b. Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia. For. Ecol. Manage. 116, 247–252.

Rice, R.E., Gullison, R.E., Reid, J.W., 1997. Can sustainable management save tropical forests? Sci. Am. 276 (4), 44–49.

Sanford, R.L., Saldarriaga, J., Clark, K.E., Uhl, C., Herrera, R., 1985. Amazon rain forest fires. Science 227, 53–55.

Smith, D.M., 1986. The Practice of Silviculture. Wiley, New York, 527 pp.

Stanley, S.A., 1999. Prescribed fire to augment the regeneration of mahogany (*Swietenia macrophylla*) and Spanish cedar (*Cedrela odorata*) in the Maya Biosphere Reserve, Guatemala. Master's Thesis. North Carolina State University, Raleigh, NC.

Stocker, G.C., 1981. Regeneration of a north Queensland rainforest following felling and burning. Biotropica 13, 86–92.

Swaine, M.D., 1992. Characteristics of dry forest in West Africa and the influence of fire. J. Veg. Sci. 3, 365–374.

Uhl, C., 1998. Perspectives on wildfire in the humid tropics. Cons. Biol. 12, 942–943.