RESPONSES OF COMMUNITY STRUCTURE AND COMPOSITION TO WILDFIRE IN DRY AND SUBHUMID TROPICAL FORESTS IN BOLIVIA

B. Mostacedo*, T. S. Fredericksen,

Proyecto BOLFOR, Santa Cruz, Bolivia. E-mail: bolfor@bibosi.scz.entelnet.bo

K. Gould

Department of Botany, University of Florida, Gainesville, Florida 32601, USA

&

M. Toledo

Proyecto BOLFOR, Santa Cruz, Bolivia. E-mail: bolfor@bibosi.scz.entelnet.bo

Received October 1999

MOSTACEDO, B., FREDERICKSEN, T. S., GOULD, K. & TOLEDO, M. 2001. Responses of community structure and composition to wildfire in dry and subhumid tropical forests in Bolivia. A comparison of plant communities within areas burned by wildfire five years previous to this study and adjacent unburned areas was conducted within a tropical subhumid and a tropical dry forest in eastern Bolivia. The objective of the study was to compare the impacts of wildfire on plant species composition, species richness and structural attributes on the two forest types. The recently logged subhumid forest was damaged more by fire than was the dry forest and had a higher increase in post-fire liana infestation. Burning altered the species composition, but to varying degrees depending on the strata or forest type. In the subhumid forest, tree species richness was lower and liana species richness higher in the burned compared to the unburned forest, whereas burning did not affect tree or liana richness in the dry forest. Conversely, shrub/sapling layer density was higher in the burned than unburned area of the dry forest but not in the subhumid forest type. For ground layer vegetation, grass and low shrub cover was greater in burned than unburned areas of both forest types. In the subhumid forest, liana cover was greater while forb and palm cover lower in the burned area. In the dry forest, tree and forb cover were higher but ground bromeliad cover lower in the burned area.

Key words: Bolivia - subhumid tropical forest - dry tropical forest - wildfire

Correspondence address: BOLFOR, Top Bol 5053, P. O. Box 52-0777, Miami, FL 33152-0777, USA

MOSTACEDO, B., FREDERICKSEN, T. S., GOULD, K. & TOLEDO, M. 2001. Tindak balas struktur dan komposisi komuniti terhadap pembakaran hutan di hutan tropika kering dan hutan sublembap di Bolivia. Perbandingan antara komuniti pokok di kawasan yang terbakar akibat kebakaran hutan lima tahun sebelum kajian ini dan di kawasan bersebelahan yang tidak terbakar telah dijalankan di hutan sublembap tropika dan hutan kering tropika di timur Bolivia. Objektif kajian adalah untuk membandingkan kesan kebakaran hutan terhadap komposisi spesies pokok, kekayaan spesies dan ciri-ciri struktur di dua jenis hutan tersebut. Hutan sublembap yang baru ditebang lebih banyak rosak akibat kebakaran berbanding hutan kering dan lebih banyak ditumbuhi liana selepas kebakaran. Kebakaran mengubah komposisi spesies, tetapi tahapnya berubah-ubah bergantung kepada strata atau jenis hutan. Di hutan sublembap, kekayaan spesies pokok lebih rendah dan kekayaan spesies liana lebih tinggi di hutan yang terbakar berbanding hutan yang tidak terbakar. Sebaliknya kebakaran tidak memberi kesan terhadap kekayaan pokok atau liana di hutan kering. Kepadatan lapisan pokok renek/anak pokok lebih tinggi di kawasan yang terbakar berbanding kawasan yang tidak terbakar di hutan kering tetapi tidak di hutan sublembap tropika. Bagi tumbuhan lapisan tanah, rumput dan penutup pokok renek yang rendah lebih banyak terdapat di kawasan yang terbakar berbanding kawasan tidak terbakar di kedua-dua jenis hutan. Di hutan sublembap, penutup liana lebih banyak didapati di kawasan yang terbakar manakala penutup herba daun lebar dan palma kurang. Di kawasan yang terbakar di hutan kering, pokok dan penutup herba daun lebar banyak didapati tetapi sebaliknya bagi penutup bromeliad tanah.

Introduction

The frequency of wildfires is increasing in Amazonian tropical forests as human populations increase in and around forested areas (Uhl & Buschbacher 1985, Holdsworth & Uhl 1997, Cochrane & Schulze 1998, Pinard *et al.* 1999). Risks and potential damage from wildfire may be particularly high in forests where logging occurs since slash from logging operations provides increased fuel to carry fires and these fires are likely to be more intense (Kauffman *et al.* 1988, Holdsworth & Uhl 1997, Cochrane *et al.* 1999). If fire becomes more frequent in forests that have evolved under conditions of low fire frequency, dramatic changes may occur with respect to the species composition, structure and economic value of forests (Holdsworth & Uhl 1997, Pinard & Huffman 1997, Uhl 1998).

The occurrence of fire and subsequent responses of plant communities may vary according to forest type. Although fire is known to have occurred in humid tropical forests, most humid forests burn very infrequently (Meggers 1987). With longer dry seasons, fire ignition and spread may be more frequent in tropical dry forests. In addition, dry forests have been subjected to higher levels of human settlement than humid forests (Murphy & Lugo 1986) and perhaps may have higher exposure rate to wildfire. Although ignition rates may be higher, impacts of fire may be smaller in dry forests if they burn more frequently and are therefore more adapted to fire. Compared to humid forests, regeneration of many dry forest species also appears to be adapted to larger-scale disturbances than those caused by natural gap dynamics such as fire (Mostacedo *et al.* 1998, Dickinson *et al.* 2001).

The Amazon Basin of Bolivia contains extensive tracts of unlogged and selectively logged forest. However, an increasing rate of human colonisation and use of forested areas are occurring (Pacheco 1998) along with a likely increase in exposure to wildfire. Tropical humid, subhumid and tropical dry forests occur in this area but wildfires may have very different impacts on these forest types. This study compared the impacts of intense wildfires in a tropical subhumid and tropical dry forest, both of which had been subjected to selective logging. Impacts measured as damage to standing trees, plant species richness and plant species composition were compared at each site using adjacent unburned areas as controls.

Materials and methods

Study sites

Las Trancas is a seasonally dry tropical forest owned and managed by the Chiquitano indigenous community within the Lomerío region south of Concepcion (16° 13' S, 61° 50' W). The altitude ranges from 410 to 470 m. Annual mean temperature in the region averages about 24.3 °C with a mean annual precipitation of about 1100 mm. Most of Las Trancas is upland forest with the 14–18 m open-canopy stratum becoming mostly deciduous during a six month dry season. The upland portions of the site include approximately 50 canopy tree species, most numerous of which are *Anadenanthera colubrina* and *Acosmium cardenasii.* Light selective logging for Spanish cedar (*Cedrela fissilis*), Spanish oak (*Amburana cearensis*) and morado (*Machaerium scleroxylon*) has been carried out at undetermined intervals on the site.

La Chonta is a timber concession located within the Guarayos Forest Reserve (15° 45' S, 62° 60' W). The site is classified as a subhumid tropical forest with a mean annual temperature of 24.5 °C and mean annual rainfall of approximately 1500 mm. Some species become deciduous during a three month dry season but most trees remain evergreen. The closed forest canopy averages 20–22 m tall and is dominated by tree species characteristic of moist forests in Bolivia, including *Hura crepitans, Ficus glabrata* and *Pseudolmedia laevis.* Selective logging of mahogany (*Swietenia macrophylla*) had been carried out just previous to the occurrence of a wildfire on this site (Ledezma, pers. comm.).

Towards the end of the dry season of 1993 (Las Trancas) and 1994 (La Chonta), intense wildfires burned large areas of forest at both study sites. Both wildfires are thought to have originated from pasture fires set to rejuvenate forage plant species for cattle. Although extensive areas of both sites were burned, the arrival of heavy rains subsequently extinguished the fire leaving areas of unburned forest similar in site characteristics and species composition to those burned before the fire. Since logging had been carried out just previous to the fire in La Chonta, fuel loads were likely much higher in that forest compared to Las Trancas. Responses of trees and vines one year after the fire at La Chonta were described by Pinard *et al.* (1999).

Sampling design and data collection

Between June and August 1998, approximately four 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 fires had passed with high intensity. Another sampling area was chosen at each site adjacent to the burned areas with respect to topography, soils and likely pre-burn vegetation composition. The only apparent difference between burned and unburned areas was that the fire was extinguished by rainfall before reaching the unburned areas. Although other fires were reported to have occurred at both sites in the past, no signs of recent fire were observed within the unburned control area at either site. Since we were comparing only one large contiguously burned or unburned area at each site, the experimental design of this study necessarily involved pseudoreplication. Nevertheless, given the difficulty of replicating wildfires in this region, we felt that it was worthwhile to compare responses to wildfire that occurred at these sites.

Within each forest type (study site), a principal transect was established through the apparent centre of the burned and unburned areas. 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 with a minimum of four sampling points (two on each side of the principal transect) along any individual transect. A total of 18 sampling points was established for each site × burn combination. This number of samples was determined largely by the length of time available for sampling. At each sampling point, plots of three different sizes were established corresponding to the size of each stratum of the plant community to be sampled including trees > 10 cm dbh (diameter at breast height), shrub/sapling layer vegetation (< 10 cm dbh, but > 2 m tall), vines and lianas moving between strata, and ground layer vegetation (< 2 m tall).

Variable-sized plots (Barbour *et al.* 1999) were established using a 10-factor prism to sample the basal area, species composition and fire damage to trees > 10 cm dbh. For each tree, measurements or observations were made for dbh, presence of bark char, height of bark char on stem (if any), tree vigour (live undamaged, live but with signs of fungal infection, standing dead), and degree of liana infestation (free of lianas, lianas ascending bole but not entering tree crown, lianas within tree crown but not completely covering crown, lianas completely covering tree crown).

Shrub/sapling stratum and vine stratum trees were sampled in one 4 × 4 m^2 plot established around the centre of each sampling point. The dbh and species of each individual stem within these plots were recorded. Understorey plants were sampled using four 1 × 1 m^2 subplots surrounding, but 1 m away from the sampling point, and dispersed along the four cardinal points of the compass. Within each subplot the percentage cover for each of the seven plant growth forms (dicot trees, palms, shrubs, vines, ground bromeliads, forbs and grasses) was ocularly estimated to the nearest 10%. The percentage of each subplot covered by woody debris > 5 cm in diameter was estimated to the nearest 10%.

Data analysis

Student's *t*-tests were used to test for differences between burned and unburned sample plots within each forest type (n = 18). The Shannon-Wiener index ($H' = -\sum P_i \, Lg_{10} P_i$) was used as an index of plant diversity (Magurran 1988). An alpha level of 0.05 was used to determine statistical differences.

Results

Damage by wildfire: tree mortality, fungal infection and liana infestation

The percentage of trees > 10 cm dbh with fire damage and the mean height of bark charring was higher in the subhumid forest than the dry forest. In addition, the difference in basal area and woody debris between burned and unburned areas was greater in subhumid forest than dry forest (Table 1). Burned areas at both sites had a proportionately greater amount of basal area in standing dead trees and trees infected with fungal rot compared to unburned areas (Figure 1). However, this proportion of dead and damaged basal area was much greater in the subhumid forest than dry forest for most tree size classes. Damage to large-diameter trees appeared to be particularly severe in the subhumid forest. Liana infestation was more severe in unburned than burned areas at both sites, with a greater percentage trees with lianas entering or covering tree crowns in unburned sites (Figures 2). In burned and unburned areas, La Chonta had more trees that were completely overtopped by lianas than did Las Trancas.

Table 1 Damage to trees (> 10 cm dbh) from wildfire in subhumid (La Chonta) and dry (Las Trancas) forests in Bolivia.

Damage variable	Subhumid forest Unburned	Subhumid forest Burned	t	p	Dry forest Unburned	Dry forest Burned	t	p
Percentage of trees with visible fire damage	0.0 (0.0)	62.0 (6.2)	10.0	< 0.001	0.0 (0.0)	11.9 (4.0)	3.0	< 0.005
Height of bark charring (cm)	0.0 (0.0)	159.0 (50.1)	10.0	< 0.001	0.0 (0.0)	94.1 (16.0)	10.0	< 0.001
Percentage cover of woody debris	0.4 (0.06)	8.8 (0.7)	2.97	< 0.01	1.9 (0.10)	5.4 (0.38)	2.1	< 0.05
Live basal area (m^2 ha^{-1})	23.2 (2.1)	10.1 (1.4)	4.93	< 0.001	22.5 (1.2)	16.3 (2.1)	2.59	< 0.01

Standard errors of means are presented in parentheses. Results of *t*-test are shown.

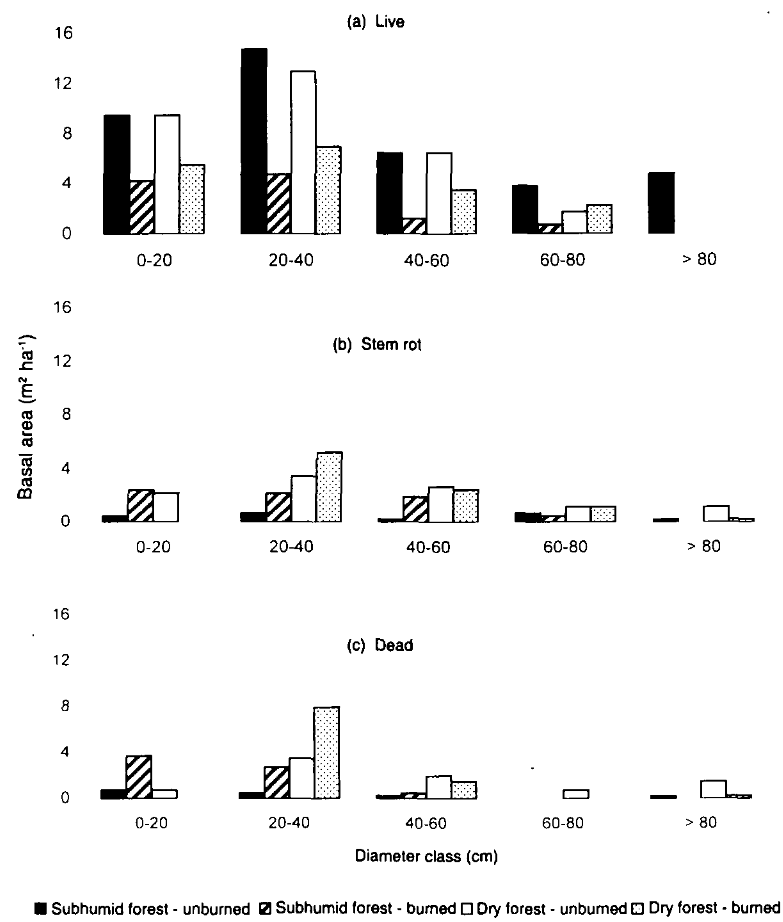

Figure 1 Basal area of live trees > 10 cm dbh (a) without stem rot, (b) with stem rot and (c) standing dead trees in an unburned tropical subhumid forest, a burned tropical subhumid forest, an unburned tropical dry forest and a burned tropical dry forest in Bolivia

Canopy and subcanopy tree species diversity and composition

Species richness and diversity of trees > 10 cm dbh in the subhumid forest were greater in the unburned compared to the burned area (Table 2). The relative basal areas of several tree species, especially the palm species *Attalea speciosa* and *A. phalerata* and the hardwood species *Amphelocera ruizii*, *Aspidosperma cylindrocarpon* and *Casearia gossypiosperma*, were greater in the burned compared to the unburned area at this site (Table 3). Pioneer species such as *Cecropia* spp., *Heliocarpus americanus* and *Zanthoxylum* sp. were also greater in the burned area of subhumid forest. The relative basal area of *Pseudolmedia laevis* was much lower and no individuals of *Cariniana ianeirensis* were found in the burned area at this site.

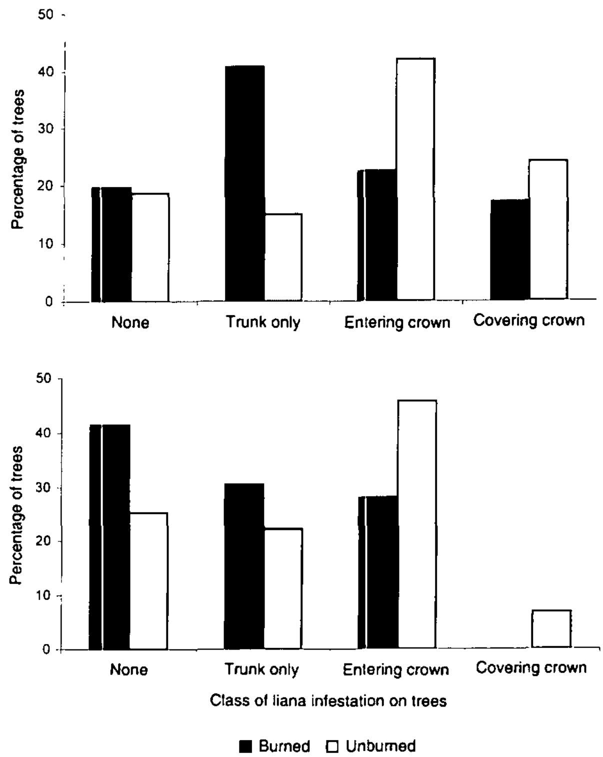

Figure 2 Liana infestation of live trees trees >10 cm dbh in (a) burned and unburned tropical sub-humid forests and (b) burned and unburned tropical dry forests in Bolivia

Table 2 Species richness (number of species) and diversity for trees (> 10 cm dbh), vines and shrub/sapling layer in plots in burned and unburned areas of a humid (La Chonta) and a dry (Las Trancas) forest in Bolivia

Life form	Species richness		Species diversity (H')	
	Unburned	Burned	Unburned	Burned
Subhumid forest				
Tree	37	26	1.52	1.00
Vine	43	67	1.49	2.73
Shrub layer	33	39	1.15	1.37
Dry forest				
Tree	25	25	1.37	1.26
Vine	42	49	1.41	1.46
Shrub layer	24	27	0.73	0.88

Data are calculated over all subplots within each treatment.

The burned and unburned sites in the dry forest had the same number of tree species with dbh > 10 cm (Table 2). The relative basal areas of the two most dominant tree species changed in the burned and unburned sites with a lower relative basal area of *Acosmium cardenasii* and a higher relative basal area of

Anadenanthera colubrina on the burned compared to the unburned area. Several shade-intolerant tree species, including *Trema micrantha, Heliocarpus americanus, Urera baccifera* and *Enterolobium contortilisiqum,* occurred in the burned area but not the unburned area of the dry forest.

Table 3 Relative basal area (RBA) of tree species (> 10 cm dbh) in areas burned by wildfire and adjacent unburned areas in a subhumid (La Chonta) and dry (Las Trancas) forest in Bolivia

Sub-humid forest		Dry forest	
Species	RBA	Species	RBA
Unburned		**Unburned**	
Pseudolmedia laevis	31.7	*Acosmium cardenasii*	35.2
Unidentified	16.8	*Anadenanthera colubrina*	14.8
Hura crepitans	9.0	*Caesalpinia pluviosa*	6.2
Terminalia spp.	6.0	*Astronium urundeuva*	4.9
Cariniana ianeirensis	3.0	*Chorisia speciosa*	4.9
Inga sp.	3.0	*Machaerium scleroxylon*	4.3
Aspidosperma sp.	2.4	*Acacia loretensis*	3.7
Myrciantes sp.	2.4	*Tabebuia impetiginosa*	3.7
Ficus glabrata	1.8	Unidentified	3.1
Ficus trigona	1.8	*Gallesia integrifolia*	1.8
Burned		**Burned**	
Hura crepitans	13.7	*Acosmium cardenasii*	23.1
Aspidosperma sp.	9.6	*Anadenanthera colubrina*	19.7
Unidentified	9.6	*Caesalpinia pluviosa*	6.0
Attalea phalerata	8.2	*Acacia loretensis*	5.1
Amptelocera ruizii	8.2	*Aspidosperma rigidum*	5.1
Casearia gossypiosperma	6.8	*Centrolobium microchaete*	5.1
Pseudolmedia laevis	4.1	*Tabebuia impetiginosa*	4.3
Pouteria sp.	4.1	*Heliocarpus americanus*	3.4
Terminalia spp.	4.1	*Copaifera chodatiana*	3.4
Astrocaryum chonta	2.7	*Platypodium elegans*	3.4

Shrub/sapling layer species diversity and composition

Plant density in the shrub/sapling layer was significantly greater in the burned compared to the unburned area at each site ($p < 0.05$) although differences were much larger between burned and unburned sites at the dry forest (Table 4). Neither species richness nor species diversity differed between burned and unburned areas in the subhumid and dry forests (Table 2). The semi-woody shrub *Costus* sp. dominated the burned and unburned areas of subhumid forest (Table 4) but *Heliconia* sp. and *Piper* sp. were more abundant in the unburned area. The shrub, *Acalypha* sp., was by far the most dominant plant in the shrub/sapling layer at the burned area of dry forest. The burned area of subhumid forest was dominated by shade-intolerant early successional genera such as *Urera, Cecropia, Zanthoxylum, Trema* and *Heliocarpus,* whereas trees in the family Lauraceae dominated the unburned area. The burned area of the dry forest had high densities of *Trema* and *Heliocarpus.* Leguminosae species were more abundant in the burned area, whereas Rubiaceae species were more abundant in the unburned area of this site.

Table 4 Actual and relative densities of the most dominant shrub/sapling layer species in burned and unburned areas of a subhumid (La Chonta) and a dry (Las Trancas) forest in Bolivia

Subhumid forest			Dry forest		
Species	Number ha^{-1}	%	Species	Number ha^{-1}	%
Unburned			**Unburned**		
Costus sp. 1	729	21.2	*Acosmium cardenasii*	243	12.5
Heliconia sp. 1	417	12.1	*Casearia aculeata*	208	10.7
Acanthaceae sp. 1	382	11.1	*Neea hermaphrodita*	174	8.9
Rubiaceae sp. 1	243	7.1	*Eugenia* sp. 1	174	8.9
Lauraceae sp. 6	208	6.1	*Opuntia brasiliensis*	174	8.9
Myristicaceae sp. 1	174	5.1	*Allophyllus edulis*	104	5.4
Sorocea sp. 1	139	4.0	*Aspidosperma rigidum*	104	5.4
Trichilia sp. 1	139	4.0	*Hybanthus* sp. 1	69	3.6
Lauraceae sp. 3	139	4.0	Rubiaceae sp. 1	69	3.6
Metrodorea sp. 1	69	2.0	*Simira* sp. 1	69	3.6
Piper sp. 1	69	2.0	*Piper* sp. 1	69	3.6
Myrtaceae sp. 2	69	2.0	*Urera baccifera*	35	1.8
Meliaceae sp. 2	69	2.0	*Nicotiana otophora*	35	1.8
Guarea sp. 1	69	2.0	*Serjania* sp. 1	35	1.8
Inga sp. 1	69	2.0	*Zanthoxylum* sp. 1	35	1.8
Other species	454	13.3	Other species	47	17.7
Total	127[a]	100.0	Total	78[b]	100
	(30)			(13)	
Burned			**Burned**		
Costus sp. 1	764	19.1	*Acalypha* sp. 1	868	25.8
Urera baccifera	590	14.8	*Neea hermaphrodita*	347	10.3
Zanthoxylum sp. 1	486	12.2	*Acosmium cardenasii*	208	6.2
Cecropia sp. 1	243	6.1	*Trema micrantha*	174	5.2
Cecropia concolor	243	6.1	*Heliocarpus americanus*	139	4.1
Heliconia sp. 1	208	5.2	*Anadenanthera macrocarpa*	139	4.1
Maranthaceae sp. 1	174	4.3	*Casearia arborea*	243	7.2
Inga sp. 1	174	4.3	*Allophyllus edulis*	104	3.1
Trema micrantha	139	3.5	*Aspidosperma cylindrocarpon*	104	3.1
Bactris major	104	3.5	*Simira* sp. 1	69	2.1
Heliocarpus americanus	69	1.7	*Trichilia elegans*	69	2.1
Solanum sp. 1	69	1.7	*Machaerium* sp.	69	2.1
Maclura tinctoria	69	1.7	*Centrolobium microchaete*	69	2.1
Jacaratia spinosa	69	1.7	*Prockia crucis*	69	2.1
Aspidosperma sp. 1	69	1.7	*Casearia gossypiosperma*	69	2.1
Other species	523	12.4	Other species	628	18.3
Total	133[a]	100.0	Total	105[a]	100
	(33)			(27)	

Means with the same letter within forest types are not significantly different at p = 0.05 using Student's *t*-test. Standard errors of means are presented in parentheses.

Vine species composition and diversity

Vine species richness and diversity were greater in the burned area of subhumid forest compared to the unburned area and similar differences were found between burned and unburned areas at the dry forest (Table 2). Overall, dry forest had over twice the vine density of that in subhumid forest (Table 5). The burned area of the subhumid forest had a significantly higher vine density than the unburned area ($p < 0.0001$) although no significant difference in vine density was observed between burned and unburned areas in dry forest. Except for *Clitostoma uleanum*, the dominant vine species in the burned and unburned area of La Chonta were different, whereas the dominant vine species in burned and unburned areas of the dry forest were more similar. An exception was the near absence of *Philodendron* sp. in the burned area of the dry forest, whereas this species was the second most abundant species in the unburned area of the same forest.

Table 5 Actual and relative densities of the most dominant vine species in burned and unburned areas of a subhumid (La Chonta) and a dry (Las Trancas) forest in Bolivia

Subhumid forest			Dry forest		
Species	Number ha^{-1}	%	Species	Number ha^{-1}	%
Unburned					
Monstera obliqua	1215	20.7	*Tinouia* sp. 1	2986	16.5
Clitostoma uleanum	903	15.4	*Philodendron* sp. 1	2431	13.4
Pleonotoma cf. *melioides*	764	13	*Serjania* sp. 1	2222	12.3
Hippocratea volubilis	417	7.1	*Hippocratea volubilis*	1771	9.8
Bignoniaceae sp. 7	313	5.3	*Arrabidaea fagoides*	1736	9.6
Cydista decora	243	4.1	*Serjania marginata*	799	4.4
Doliocarpus sp. 1	139	2.4	*Cydista decora*	799	4.4
Melloa sp. 1	139	2.4	Malpighiaceae sp. 3	660	3.6
Celtis iguanaea	104	1.8	*Trigonia boliviana*	590	3.3
Cissus sicyoides	104	1.8	*Perianthomega vellozoi*	451	2.5
Sapindaceae sp. 5	104	1.8	*Clitostoma binatum*	382	2.1
Malpighiaceae sp. 1	104	1.8	*Forsteronia pubescens*	382	2.1
Fevillea pergamentacea	104	1.8	Malpighiaceae sp. 4	347	1.9
Trigonia boliviana	69	1.2	*Clitostoma uleanum*	347	1.9
Sapindaceae sp. 1	69	1.2	*Arrabidaea binatum*	382	2.1
Other species	1079	18.2	Other species	1805	10.1
Total	150[b]	100	Total	431[a]	100
	(41)			(110)	
Burned					
Clitostoma uleanum	1042	10.5	*Tinouia* sp. 1	4063	21.5
Convolvulaceae sp. 1	590	5.9	Malpighiaceae sp. 4	2049	10.9
Laciasis sorghoidea	556	5.6	*Hippocratea volubilis*	1424	7.6
Unidentified sp. 05	486	4.9	*Amphilopium* sp.	1111	5.9
Serjania marginata	451	4.5	*Philodendron* sp. 1	1042	5.5
Unidentified sp. 06	451	4.5	Sapindaceae sp. 1	1007	5.5
Acacia sp. 1	382	3.8	*Serjania marginata*	799	4.2
Cissus sicyoides	382	3.8	*Serjania* sp. 1	799	4.2
Phaffia sp. 1	347	3.5	Malpighiaceae sp. 3	556	2.9
Pleonotoma cf. *melioides*	347	3.5	Sapindaceae sp. 2	521	2.8
Hippocratea volubilis	313	3.1	*Serjania* sp. 2	521	2.8
Monstera obliqua	313	3.1	*Manaosella* cordifolia	486	2.6
Trigonia boliviana	278	2.8	*Trigonia boliviana*	451	2.4
Cissampelos tropaeolifolia	243	2.4	*Arrabidaea fagoides*	382	2.0
Stizophyllum inaequilaterum	243	2.4	Malpighiaceae sp. 1	278	1.5
Other species	3541	35.7	Other species	3365	15.1
Total	199[a]	100	Total	385[a]	100
	(27)			(97)	

Means with the same letter within forest types are not significantly different at $p = 0.05$.
Standard errors of means are presented in parentheses.

Ground layer species composition

Total ground layer plant cover (< 2 m tall) did not differ among burned and unburned areas at either site. However, percentage cover varied between burned and unburned areas for different plant life forms (Table 6). Low shrub cover and grass cover were higher in burned than unburned areas at each site. In dry forest, trees and herb cover were higher in the understorey of burned areas than unburned areas, while burned plots had significantly less ground bromeliad cover than unburned plots. In subhumid forest, both palm and liana covers were significantly higher in burned areas, while herb cover was significantly higher in unburned areas.

Table 6 Mean percent cover of plant life forms in the forest ground layer (< 2 m tall) of burned and unburned areas of a subhumid (La Chonta) and a dry (Las Trancas) forest in Bolivia

Life form	Subhumid forest				Dry forest			
	Unburned	Burned	t	p	Unburned	Burned	t	p
Dicot tree	9.7 (3.2)	10.2 (2.5)	0.12	0.90	4.4 (1.4)	13.0 (1.8)	4.22	< 0.001
Palm	3.1 (1.3)	7.5 (2.0)	1.83	0.07	0.0 (0.0)	0.0 (0.0)	0.00	1.00
Shrub	7.0 (1.4)	12.0 (3.7)	1.28	0.21	20.5 (3.7)	33.0 (3.5)	2.48	0.02
Vine	23.3 (4.7)	38.6 (4.3)	2.40	0.02	31.3 (3.2)	32.3 (4.4)	0.35	0.72
Forb	72.2 (4.6)	44.1 (5.8)	3.81	< 0.001	11.8 (3.5)	23.4 (3.6)	2.32	0.03
Grass	7.4 (1.1)	23.8 (3.3)	4.74	< 0.001	1.0 (0.6)	3.3 (1.1)	1.86	0.07
Ground bromeliad	0.0 (0.0)	0.0 (0.0)	0.00	1.0	43.4 (5.3)	17.0 (5.3)	1.16	< 0.001
Total	86.5 (3.2)	87.4 (3.5)	0.18	0.86	78.9 (2.7)	83.6 (3.0)	1.16	0.63

Standard errors of means are presented in parentheses.

Discussion

Wildfires had a significant impact on the structure, species composition and diversity of both subhumid and dry forests in this study. Wildfires caused mortality of canopy and subcanopy trees, induced stem rot in many trees that survived, as well as promoted the dominance of early successional and fire-tolerant species. However, the wildfire in the subhumid forest was more intense than the dry forest, as evident through increased bark charring heights. In addition, the impacts of fire were greater relative to unburned controls in tree mortality and changes in vegetation composition.

Neither of these forests is believed to have frequent fires, although the fire frequency is not known at either site. La Chonta is surrounded by agricultural and pastoral land and experiences the threat of wildfire each dry season. However, intense wildfires such as that of 1995 are considered rare and likely resulted from the combination of an unusually severe dry season as well as input of slash from prior logging (Ledezma, pers. comm.). Severe dry seasons can create conditions for fires in forests not ordinarily susceptible to burning (Nepstad *et al.* 1998) especially if logging had been carried out previously in the forest (Uhl & Kauffman 1990, Holdsworth & Uhl 1997). In Las Trancas, Pinard and Huffman (1997) estimated that fire had not occurred in this forest within 40 years based on wood samples and interviews with local residents, although slash and burn agriculture commonly occurs in forests adjacent to nearby communities.

Comparisons of fire impacts between different tropical forest types are difficult because previous fire history, weather conditions and fuel loads irrespective of forest type are important in influencing fire behaviour (Pinard *et al.* 1999). However, in a study of wildfire in Brazil, it was observed that fire in high, closed-canopy forests was largely restricted to the ground vegetation layer, killing small trees, but leaving larger trees intact (Uhl & Buschbacher 1985). In lower, open-canopy forests, fires burned into crowns, resulting in extensive damage. Also low-canopy forests often have high densities of vines before the initiation of fires and a much higher vine proliferation as well as lower tree and forb regeneration following fires compared to closed-canopy forests. The high, closed-canopy subhumid forest of La Chonta sustained proportionately greater damage to large trees, had greater increase in vine proliferation and had lower recruitments of tree regeneration and forbs than the low, open-canopy dry forest in Las Trancas. While the ignition and spread of wildfire may normally be more difficult in the subhumid forest of La Chonta compared to the dry forest of Las Trancas, previous logging may have reversed this trend, resulting in the greater fire intensity and resultant impacts observed in La Chonta.

Proliferation of lianas (woody vines) following wildfire has been noted in several studies (Woods 1989, Pinard *et al.* 1999). However, liana densities in burned and unburned areas of dry forest were similar. Like trees, many lianas are able to sprout vigorously from intact root systems following fire, giving them an early competitive advantage in recolonisation of burned sites. In the subhumid forest, lianas have quickly dominated the burned area of this site and have since maintained nearly constant densities. Liana density one year after the fire in the subhumid forest (La Chonta) is 10 900 stems ha^{-1} (Pinard *et al.* 1999) and at year four is 9965 stems ha^{-1}. Wildfire actually reduced the infestation of standing trees compared to unburned areas at both sites but increases in liana regeneration in the subhumid forest will likely reverse this pattern in the future.

Despite differences previously described, similarities in the impacts of wildfire were observed at these sites. Wildfire increased invasion of successional species that regenerate from resprouting and species with thicker fire resistant bark. The rapid appearance of early successional species in burned areas at both sites such as *Cecropia, Urera* and *Heliocarpus* was likely the result of germination from soil seed banks (Uhl & Clark 1983), or perhaps via volant seed dispersers such as birds and bats (Uhl & Jordan 1984). Despite the abundance of these successional species in the years following fire they are likely to quickly disappear from these areas as succession proceeds on these sites.

The subsequent successional pathways following fire at the two sites are uncertain, but may be shifted towards species with greater resprouting capacities. After a fire in a moist forest in the eastern Amazon, Kauffman (1991) reported that 59% of the tree species were capable of resprouting after fire, although the percentage of stems resprouting for individual tree species was variable. The relatively high abundance of some species in the burned area of Las Trancas may be related to resprouting ability; an example being *Centrolobium microchaete* whose regeneration is dominated by sprouting as opposed to seed (Fredericksen *et al.* 2000).

In sampling damage to trees one year after the fire in La Chonta, Pinard *et al.* (1999) found that one-third of the trees surviving the fire had basal damage to the cambium, which likely explained the similar percentage of the basal area of trees with fungal rot in La Chonta. Trees that are most likely to die and succumb to fungal attack are species with thinner bark that makes them prone to cambial death during fire (Uhl & Kauffman 1990, Pinard & Huffman 1997). In the burned subhumid forest of La Chonta, thin-barked trees, relatively common in the unburned forest, were either rare or absent. These species included *Inga, Cariniana* spp. and *Pseudolmedia laevis.* Pinard *et al.* (1999) did not report high mortalities for these species one year following the fire. Nevertheless, damage sustained from fire may not occur rapidly, but rather over a number of years after the fire (Uhl & Buschbacher 1985). The greater cover of palms in the burned compared to the unburned areas of La Chonta may be attributed to their monocot vascular anatomy with cambial tissue imbedded deep within the stem (Uhl & Kauffman 1990). Palms are usually absent in the dry forests of Las Trancas outside of gallery forests surrounding rivers and seasonal streams.

Plant species composition for shrub/sapling and ground vegetation strata in burned and unburned areas differed significantly between forest types. Changes in species composition in these strata may imply differences in post-fire successional pathways for the two forest types. In La Chonta, density of shrub/sapling layer plants was only slightly greater in burned compared to unburned plots, while burned plots had a 73% greater shrub/sapling layer density than unburned plots in Las Trancas. Within this strata of burned plots in Las Trancas the numbers of commercially valuable tree species (*Anadenanthera colubrina, Centrolobium microchaete* and *Cedrela fissilis*) are higher than in unburned plots. Similar increases in commercial tree regeneration have been observed in logging gaps receiving controlled burning (Kennard 2000). The apparent removal of ground bromeliads by fire in Las Trancas may partially explain the higher regeneration success at burned plots. Dense colonies of ground bromeliads significantly inhibit tree regeneration (Fredericksen *et al.* 1999). In La Chonta, stems of commercially valuable tree species were absent from both burned and unburned plots. Based on these results, fire may have a positive effect on the future economic value of Las Trancas but neither increased nor decreased advanced regeneration at La Chonta.

Setting fires to maintain pasture grasses is a common practice in Bolivia and elsewhere in the Amazonian forests. When these fires spread into recently logged forests, they often burn more readily and intensely than unlogged forests because of large amounts of logging slash and better fuel drying in canopy openings (Uhl & Buschbacher 1985, Kauffman *et al.* 1988). The results of this study confirmed the extensive ecological and economic damage caused by fires in other Amazonian forests (Uhl & Buschbacher 1985, Uhl 1998, Cochrane *et al.* 1999). However, these results also suggested that subhumid forests might be equally or more vulnerable to fire damage compared to dry forests, at least where logging resulted in large quantities of woody fuels or during periods of extreme drought. Since they burn less frequently and are therefore less likely to be adapted to fire than dry forests, damage in subhumid forests may also be more severe.

Acknowledgements

This study was funded by Proyecto BOLFOR, a USAID sustainable forestry mangement project in Bolivia. We thank D. Kennard and J. Nittler for their review of drafts of this manuscript and D. Nash for his invaluable help with language translations.

References

BARBOUR, M. G., BURK, J. H., PITTS, W. D., GILLIAM, F. S. & SCHWARTZ, M. W. 1999. *Terrestrial Plant Ecology.* 3rd Edition. Benjamin/Cummings Publishing, Merlo Park. 649 pp.

COCHRANE, M. A. & Schulze, M. D. 1998. Forest fires in the Brazilian Amazon. *Conservation Biology* 12: 948–950.

COCHRANE, M. A., ALENCAR, A., SCHULZE, M. D., SOUZA, C. M., NEPSTAD, D. C., LEFEBVRE, P. & DAVIDSON, E. A. 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* 284: 1832–1835.

DICKINSON, M. B., WHIGHAM, D. F. & HERMANN, S. M. 2001. Tree generation in felling and natural disturbance in a semi-decidous tropical forest in Mexico. *Forest Ecology Management* 134: 137–151.

FREDERICKSEN, T. S., JUSTINIANO, J., MOSTACEDO, B., KENNARD, D. & MCDONALD, L. 2000. Regeneration ecology of three leguminous timber species in a Bolivian dry forest. *New Forests* 20: 45–64.

FREDERICKSEN, T. S., MCDONALD, L., WRIGHT, K. & MOSTACEDO, B. 1999. Ecología de la bromeliácea terrestre *Pseudananas sagenarius*, (Bromeliaceae, Bromelioideae) en bosques secos de Bolivia. *Boletín de Sociedad Boliviana Botánica* 2: 165–173.

HOLDSWORTH, A. R. & UHL, C. 1997. Fire in Amazonian selectively logged rain forest and the potential for fire reduction. *Ecological Application* 7: 713–725.

KAUFFMAN, J. B. 1991. Survival by sprouting following fire in tropical forests of the eastern Amazon. *Biotropica* 23: 219–224.

KAUFFMAN, J. B., UHL, C. & CUMMINGS, D. 1988. Fire in the Venezuelan Amazon. Part 1: fuel biomass and fire chemistry in the evergreen rain forest of Venezuela. *Oikos* 3: 167–175.

KENNARD, D. 2000. Regeneration of commercial tree species following controlled burning in a tropical dry forest in eastern Bolivia. Ph.D. dissertation, University of Florida, Gainesville. 110 pp.

MAGURRAN, E. A. 1988. *Ecological Diversity and its Measurement.* Princeton University Press, Princeton, 200 pp.

MEGGERS, B. J. 1987. The early history of man in Amazonia. Pp. 151–174 in Whitmore, T. C. & Prance, G. T. (Eds.) *Biogeography and Quaternary History in Tropical America.* Clarendon Press, Oxford.

MOSTACEDO, C. B., FREDERICKSEN, T. S. & TOLEDO, M. 1998. Respuestas de las plantas a la intensidad de aprovechamiento en un bosque semideciduo pluviestacional de la región de Lomerío, Santa Cruz, Bolivia. *Rev. Soc. Boliviana Bot.* 2: 75–88.

MURPHY, P. G. & LUGO, A. E. 1986. Ecology of tropical dry forests. *Annual Review of Ecology and Systematic* 17: 67–88.

NEPSTAD, D., MOREIRA, A., VERÍSSIMO, A., LEFEBVRE, P., SCHLESINGER, P., POTTER, C., NOBRE, C., SETZER, A., KRUG, T., BARROS, A. C., ALENCAR, A., PEREIRA, J. R. 1998. Forest fire prediction and prevention in the Brazilian Amazon. *Conservation Biology* 12: 951–953.

PACHECO, P. 1998. *Estilos de desarrollo, deforestación, y degradación de los bosques en las tierras bajas de Bolivia.* CIFOR/CEDLA/TIERRA, La Paz, Bolivia. 389 pp.

PINARD, M. A. & HUFFMAN, J. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. *Journal of Tropical Ecology* 13: 727–740.

PINARD, M. A., LICONA, J. C. & PUTZ, F. E. 1999. Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia. *Forest Ecology Management* 116: 247–252.

UHL, C. 1998. Perspectives on wildfire in the subhumid tropics. *Conservation Biology* 12: 942–943.

UHL, C. & BUSCHBACHER, R. J. 1985. A disturbing synergism between cattle ranch burning practices and selective tree harvesting in the eastern Amazon. *Biotropica* 17: 265–268.

UHL, C. & CLARK, K. 1983. Seed ecology of selected Amazon basin successional species. *Botanical Gazette* 144: 419–425.

UHL, C. & JORDAN, C. F. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. *Ecology* 65: 1476–1490.

UHL, C. & KAUFFMAN, J. B. 1990. Deforestation, fire susceptibility and potential tree responses to fire in the eastern Amazon. *Ecology* 71: 437–449.

WOODS, P. 1989. Effects of logging, drought and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* 21: 290–298.