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Effects of high- and low-intensity fires on soil properties and plant growth in a Bolivian dry forest

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Abstract

We compared soil nutrient availability and soil physical properties among four treatments (high-intensity fire, low-intensity fire, plant removal, and harvesting gap) and a control (intact forest understory) over a period of 18 months in a tropical dry forest in Bolivia. The effect of treatments on plant growth was tested using a shade intolerant tree species (*Anadenanthera colubrina* Vell. Conc.) as a bioassay. Surface soils in high-intensity fire treatments had significantly greater pH values, concentrations of extractable calcium (Ca), potassium (K), magnesium (Mg), and phosphorus (P), and amounts of resin-available P and nitrogen (N) than other treatments; however, a loss of soil organic matter during high-intensity fires likely resulted in increased bulk density and strength, and decreased water infiltration rates. Low intensity fires also significantly increased soil pH, concentrations of extractable Ca, K, Mg, and P, and amounts of resin-available P and N, although to a lesser degree than high-intensity fires. Low-intensity fires did not lower soil organic matter contents or alter soil physical properties. Plant removal and harvesting gap treatments had little effect on soil chemical and physical properties. Despite the potentially negative effects of degraded soil structure on plant growth, growth of *A. colubrina* seedlings were greater following high-intensity fires. Evidently, the increase in nutrient availability caused by high-intensity fires was not offset by degraded soil structure in its effects on seedling growth. Long-term effects of high intensity fires require further research.

Introduction

Prescribed burns produce several effects that are beneficial for the regeneration of shade-intolerant tree species, including vegetation removal, mineral soil exposure, and nutrient release (Bond and van Wilgen, 1996; Hungerford et al., 1990). Yet, the effects of prescribed burns on above- and below-ground processes vary widely, depending largely on the intensity of the fire (Bond and van Wilgen, 1996; Moreno and Oechel, 1994). While most studies of low to moderately intense fires report increases in available nutrients (DeBano et al., 1977; reviews by Dunn et al., 1977; Ewel et al., 1981; Humphreys and Craig, 1981; Hungerford et al., 1990; Neary et al., 1999; Wells et al., 1979; Wright and Bailey, 1982), intense fires may cause a net loss of nutrients from the forest system through volatilization, ash transport, and run-off (DeBano et al., 1977; Giovannini et al., 1990). Intense burns may also alter soil structure and texture (Dyrness and Youngberg, 1957; Ulery and Graham, 1993) resulting in increased soil bulk density (DeByle, 1981), and reduced soil porosity, water infiltration rates, and water holding capacity (Wells et al., 1979).

The changes in chemical and physical soil properties caused by fire may have important consequences for growth of tree seedlings. Increased nutrient availability after fire may benefit plant growth if nutrients are limiting prior to burning (Hungerford et al., 1990). On the other hand, seedling growth in intensely burned soils may be slowed due to high pH and toxic levels of minerals (Giovannini et al., 1990). Altered soil physical properties, such as soil strength, bulk density, and water infiltration rates, may also impair plant growth.

Plant uptake of nutrients and water is slowed in structurally degraded soils through the combined effects of lower soil moisture and lower soil porosity (Nye and Tinker, 1977). Mechanical impedance of root growth caused by increased bulk density and soil strength (Gerard et al., 1982) also slows nutrient and water uptake. Therefore, the benefit of controlled burns for tree seedling growth may ultimately depend on fire intensity; after intense fires the advantages of increased nutrient availability may be offset by degraded soil structure.

We examined the effects of prescribed burns of high and low intensities on soil properties and tree seedling growth in a tropical dry forest in lowland Bolivia. This particular forest region has been commercially managed for timber by the Chiquitano indigenous group since 1982 (McDaniel, 2000). Of the 17 timber species harvested from these forests, more than half are shade intolerant and regenerate poorly following selective logging. Fire, of both natural and anthropogenic origins, has likely been a pervasive influence on these dry forests (Kennard, 2000) and, therefore, forest managers have begun to explore prescribed burning as a silvicultural tool to enhance the regeneration of these shade-intolerant species.

This experiment is part of a larger study that examined the effects of fire intensity on soils, commercial tree regeneration, and plant diversity (Kennard, 2000). In this paper, we describe the effects of high and low-intensity prescribed burns on soil nutrient availability and soil physical properties. Using a bioassay, we discuss how these treatment-induced changes in soil properties may influence tree seedling growth. We hypothesized that while low intensity fires may benefit plant growth due to an increase in nutrient availability, intense fires may impair plant growth by damaging soil structure.

Materials and methods

Study site

This study was conducted in the Lomerio Community-owned Forest, Province of Nuflo de Chavez, Department of Santa Cruz, Bolivia (16°45′S, 61°45′W). Lomerio is situated in the heart of Chiquitania, which lies in the transition zone between the humid forests on the southern rim of the Amazon basin and the thorn scrub formations of the Gran Chaco. The natural vegetation is classified as tropical dry forest (*sensu* Holdridge et al., 1967). The regional climate is characterized by a strong dry season from May–October. The mean annual temperature at Concepcion is 24.3°C with temperatures that vary between 3 (July) and 38.1°C (October, Killeen et al., 1990). Mean annual precipitation is 1129 mm. The landscape is dominated by low hills composed of granite, gneiss, and metamorphic rocks of Precambrian origin (Geobold, 1981) punctuated by exposed granitic outcrops (inselbergs). The soils of the area are classified as Inceptisols and Oxisols (Ippore, 1996). Elevation varies between 400 and 600 m a.s.l.

Lomerio consists of 27 Chiquitano communities with a total population of approximately 5000. The Chiquitanos of Lomerio have been managing their forests for timber since 1982 with technical and financial support from several international institutions (e.g., APCOB, BOLFOR). Forestry operations of the Chiquitano communities were certified by the SmartWood Program of Rainforest Alliance in 1995. This study was conducted in a management unit near the community of Las Trancas that was selectively harvested in 1997 (harvesting intensity of 4.4 m^3 ha^{-1}).

Experimental design and treatments

In June of 1997, 16 recently formed felling gaps meeting the following criteria were located for study: canopy gap area between 200–600 m^2, slopes no greater than 15°, less than 20% rock outcrops, no trees >40 cm DBH within gap area, and not located in the path of skid trails. Each gap was divided into four 10 × 10 m plots by cardinal axes originating from the gap center. Existing gap area was enlarged to a uniform 20 × 20 m area by cutting all vegetation >2 m tall (*sensu* Brokaw, 1985) by machete or chainsaw. One of four treatments was randomly assigned to each 10 × 10-m plot within each gap: (1) high-intensity burn; (2) low-intensity burn; (3) above-ground plant and coarse debris removal (hereafter referred to as plant removal); and (4) a gap control. A forest plot was located ~20–25 m from each gap in unlogged forest.

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

Slash was left for five rainless weeks to dry and prescribed burns were conducted from August 29 to September 1, 1997, near the end of the 5-month dry season. A circular ignition technique was used for both burn treatments. Maximum soil temperature during burns was measured at 0- and 3-cm depths using temperature indicating paints (Tempilaq®, Tempil. Division. Air Liquide America Corporation, South Plainfield, NJ, USA). Fire intensity was estimated by Beaufait's (1966) technique which calculates total energy output from the amount of water vaporized from cans during burns as:

total energy output = [(80 cal/g water) × (g water)] + [(540 cal/g water) × (g water)]

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

Soil chemical properties

Within 2 days following controlled burns, the mass of ash deposited during high-intensity burns was estimated by collecting and weighing all ash on the soil surface in a 1-m^2 area, in a reduced sample of three high-intensity burn plots (ash deposited during low-intensity burns was negligible and therefore was not measured). Composite ash samples were collected from each plot and used to measure pH and mineral element concentrations. Ash pH was determined as for soil pH, described below. To determine nutrient concentrations, 0.5 g of ash was heated in 10 ml of 1 M HNO_3 and then resolubilized in 10 ml of 1 M HCl. Extracts were then analyzed for Ca, K, Mg, and P at the Analytical Research Laboratory at the University of Florida with an ICAP Spectrometer (Thermo-Jarrell Ash Corporation, Franklin, MA).

Soil samples (0–8 cm depth) were collected from each treatment and forest plot (n = 16 blocks) at 2, 6, 9, 12 and 18 months after burns; additional samples from 8 to 20 cm depth were collected after 9, 12, and 18 months. Each sample (250 g) was a composite of soil from four randomly selected sites in each plot. Soil pH was determined with a hand-held meter (Oakton® pHTestr 3) on a solution of 20 g fresh soil:50 ml of distilled water (Anderson and Ingram, 1993). Soil samples were then air-dried in the field to a constant weight, sieved, and stored in a cool dry area until transported to the University of Florida for chemical analyses. Ca, K, Mg, and P were extracted with Mehlich-I solution: 0.05 M HCl and 0.0125 M H_2SO_4 (Hanlon et al., 1994). Extracts were then analyzed by ICAP spectroscopy. Soil organic matter content was analyzed using the Walkley-Black dichromate method (Hanlon et al. 1994). A subset of 24 soil samples (0–8 cm depth) was tested for total nitrogen using an elemental analyzer (Carloerba NCS 2500).

Resin-available nitrogen ($NH_4{}^+$-N and $NO_3{}^-$-N) and phosphorus ($PO_4{}^{-3}$-P) in each treatment were estimated by burying anion and cation exchange resin bags at 5 cm depth. Resin bags were prepared by enclosing 5.0 g (moist weight) of either anion exchange resins (Sigma-Dowex®) or cation exchange resins (Fisher Scientific®) in bags of nylon stocking material sewn closed with nylon thread. Before burial, resin bags were hydrated overnight with dionized water. Four bags of each resin type were buried per treatment plot (4 bags × 2 resin types × 5 treatments × 16 blocks). Three rotations of resins were buried to include the first and second rainy seasons following burns (November 1997–January 1998 and December 1998–February 1999, respectively) and the transition from the first rainy season to the first dry season (May–July 1998). After removal from the field, resin bags were kept cool (refrigerated when possible) until transported to the University of Florida for analysis. For each resin type, the four bags per treatment plot were pooled and 12 g of resin subsampled and extracted in 120 ml of 2 M KCl for 24 h. Extractions were analyzed for amonium-N and nitrate-N using automated spectrophotometry (Flow IV Ion Analyzer, AlpKem (O-I-Analytical), College Station, TX). Extracts from anion exchange resins were diluted with distilled water to 1 M KCl and analyzed for $PO_4{}^{-3}$-P using the atomic emission spectrometric method (Thermo-Jarrell Ash Corp, Franklin, MA).

Soil physical properties

Compressive soil strength was estimated with a pocket penetrometer (Forestry Suppliers®) at 2, 6, 9, and 12 months following burns. Soil strength readings were taken at four randomly selected points in each treatment and forest plot from all 16 blocks (n = 16). Soil bulk density (air-dry) of the surface 7 cm was estimated 6 and 12 months following burns in a reduced sample of 10 blocks (n = 10). Water infiltration rates were estimated 8 months following burns in a reduced sample of 4 blocks (n = 4) using a modified version of the single ring method (Anderson and Ingram, 1993). In each gap treatment and forest site, a point was randomly located, cleared of surface litter, and a graduated PCV cylinder (10 cm diameter, 25 cm length) inserted 10 cm into the soil. The cylinder was filled with water to 10 cm and timed until the water level dropped to 5 cm. This process was repeated three times and infiltration rates calculated separately for each repetition (i.e., the first, second, and third 5 cm increments of water) as the volume flux of water flowing into the soil profile per unit surface area (ml cm^{-2} s^{-1}; Hillel, 1982).

Plant growth

We examined the effect of high and low intensity burns on plant growth using a commercial timber species as a bioassay. *Anadenanthera colubrina* (Vell. Conc.), a shade-intolerant tree species, is the most common and dominant timber species in Lomerio. Four weeks after the experimental fires, collected seeds of *A. colubrina* were placed in four 4-m^2 subplots in each treatment and forest understory plot (20 seeds/plot = 5 seeds/m^2). Seedfall of *A. colubrina* was extremely abundant in 1997 (~4 seeds/m^2), and therefore seedlings arising from naturally dispersed seeds were sampled as well as seedlings arising from collected seeds. In each subplot, three randomly selected seedlings were tagged (three seedlings per subplot × four subplots per treatment plot = 12 seedlings per treatment plot) and seedling height (height to apical meristem) measured 1.5, 3, 6, 9, 12, and 18 months after burns.

Statistical analyses

Soil pH, moisture content, Mehlich-I extractable elements, organic matter content, resin-available N and P, soil strength, and seedling height were analyzed using an ANOVA with repeated measures. Treatment was a fixed effect and block a random effect in each model. Soil properties were log transformed for analyses when not normally distributed, but all values presented in the text are non-transformed. Where a significant time × treatment interaction was found, variables were analyzed separately by month. Statistically significant differences ($P < 0.05$) were further analyzed with Tukey's HSD multiple comparisons. Square-transformed values of bulk density were compared among treatments using an ANOVA with treatment and month as fixed effects and blocks as a random effect, followed by Tukey's HSD multiple comparisons. Log transformed rates of infiltration were compared among treatments using an ANOVA with treatments and repetitions (i.e., each 5-cm increment) as fixed effects and blocks as random effects.

Results

Burn characteristics

Temperatures at the soil surface during high-intensity fires averaged 704 ± 42°C (x ± S.E., n = 16). The highest temperature measured was 927°C. Temperature at 3 cm depth averaged 227 ± 27°C (n = 16). Fire intensities ranged from 152 to 3795 kcal and averaged 1627 ± 241 kcal (n = 15). Flame heights ranged from 1.5 to 5 m.

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

Treatment effects on soil properties

Ash deposited during high-intensity fires averaged 4.8 ± 0.3 cm in depth (n = 16) and 1.5 ± 0.6 kg/m^2 (n = 3) in mass. Ash samples had an average pH of 10.7 ± 0.1 (n = 16) and cation concentrations of 353 mg Ca/g, 17.5 mg Mg/g, 61 mg K/g, and 4.8 mg P/g.

High-intensity fires significantly increased P, Mg, K, and Ca concentrations in the top 8 cm of soil, but the magnitude and its change over time varied by nutrient (Fig. 1 and Table 1). These increases were also detected at 8–20 cm for all elements except Mg (Table 2), although differences were smaller than in

Table 1. Results of ANOVAs of soil nutrients, organic matter, water content, and soil pH of soil sampled 0–8 cm in four gap treatments and forest plots at 5 times following burns. All variables were log transformed. Where a significant time × treatment interaction was found, variables were analyzed separately by month. Treatments with different letters are significantly different at $P<0.05$

No interaction time × treatment				Post-hoc test results					
Variable	Factor	*F*	*P*	Month	High	Low	Removal	Control	Forest
Magnesium	Treatment	23.3	<0.001	3	a	b	c	c	c
	Time	8.7	<0.001	6	a	b	bc	c	c
				9	a	b	bc	c	c
				12	a	b	c	c	c
				18	a	b	b	b	b
Calcium	Treatment	70.1	<0.001	3	a	b	c	c	c
	Time	3.0	0.026	6	a	b	bc	c	bc
				9	a	b	b	b	b
				12	a	b	b	b	b
				18	a	a	a	a	a
Water content	Treatment	3.9	0.008	3	ab	a	a	a	b
	Time	39.0	<0.001	6	ab	ab	a	ab	b
				9	a	a	a	a	b
				12	a	a	a	a	a
				18	a	a	a	a	a

Significant time × treatment interaction				Post-hoc test results				
Variable	Month	*F*	*P*	High	Low	Removal	Control	Rorest
Potassium	3	77.4	<0.001	a	b	c	c	c
	6	64.1	<0.001	a	bc	c	bc	b
	9	11.5	<0.001	a	bc	c	b	bc
	12	7.8	<0.001	a	b	b	ab	a
	18	3.7	0.009	ab	b	b	ab	a
Phosphorus	3	167.5	<0.001	a	b	c	c	c
	6	60.8	<0.001	a	a	b	b	b
	9	45.5	<0.001	a	b	c	c	c
	12	58.7	<0.001	a	b	c	c	c
	18	37.2	<0.001	a	b	c	c	c
Organic matter	3	7.3	<0.001	a	b	b	b	b
	6	15.9	<0.001	a	b	b	b	b
	9	4.6	0.003	a	b	b	ab	ab
	12	4.7	0.002	a	b	ab	ab	b
	18	3.9	0.007	ab	ab	b	ab	a
Soil strength	3	12.6	<0.001	a	b	b	b	b
	6	24.3	<0.001	a	a	a	b	c
	9	28.8	<0.001	a	b	b	c	c
	12	16.9	<0.001	a	bc	b	c	c

Table 2. Results of ANOVAs of soil nutrients, organic matter, water content, and soil pH in the 8–20 cm depth of soil of four gap treatments and forest plots at 3 times following burns. All variables were log transformed. Where a significant time × treatment interaction was found, variables were analyzed separately by month. Treatments with different letters are significantly different at $P<0.05$

No interaction time × treatment				Post-hoc test results					
Variable	Factor	*F*	*P*	Month	High	Low	Removal	Control	Forest
Phosphorus	Treatment	105.4	<0.001	9	a	b	bc	bc	bc
	Time	59.4	<0.001	12	a	b	bc	bc	bc
				18	a	b	b	b	b
Magnesium	Treatment	2.1	0.09	9					
	Time	7.3	0.001	12					
				18					
Calcium	Treatment	10.5	<0.001	9	a	b	b	b	b
	Time	4.7	0.013	12	a	ab	b	b	b
				18	a	b	ab	b	b
Water content	Treatment	5.6	0.001	9	a	a	a	a	b
	Time	51.2	<0.001	12					
				18	ab	ab	a	ab	b
pH	Treatment	70.9	<0.001	9	a	b	bc	c	bc
	Time	58.9	<0.001	12	a	b	c	c	c
				18	a	b	c	c	c

Significant time × treatment interaction				Post-hoc test results				
Variable	Month	*F*	*P*	High	Low	Removal	Control	Rorest
Potassium	9	34.6	<0.001	a	b	c	bc	bc
	12	17.5	<0.001	a	b	b	b	b
	18	9.5	<0.001	a	b	b	b	ab
Organic matter	9	1.7	0.16					
	12	2.7	<0.001	a	ab	ab	b	ab
	18	11.3	<0.001	b	b	a	c	c

surface soils. Low-intensity fires also significantly increased P, Mg, K, and Ca in the top 8 cm of soil, although increases were smaller than in high-intensity fire plots, did not persist as long, and were not detected at 8–20 cm. Plant removal and gap control treatments had no detectable effect on P, Mg, K, and Ca at either soil depth.

Both high- and low-intensity fires significantly increased resin-available NH_4^+-N (F = 58.7, P = <0.001), NO_3^--N ($F = 6.3$, $P = 0.001$), and PO_4^{-3}-P (F = 12.2, P = <0.001) during the first rainy season following burns (Fig. 2). Other than an increase in NO_3^--N in plant removal treatments during the first rainy season, the remaining treatments had little effect on NH_4^+-N, NO_3^--N, and PO_4^{-3}-P availability.

Soil pH after high-intensity fires at 0–8 and 8–20 cm was greater than in all other treatments throughout the 18-month sampling period (Fig. 3 and Tables 1 and 2). After low-intensity fires, soil pH was greater than in the remaining treatments at both depths at all sampling periods. The plant removal and gap control treatments had little effect on soil pH.

High-intensity fires significantly lowered soil organic matter content in surface soils; 2 months following after fires soil organic matter in the top 8 cm of soil was approximately 72% that of forest soils (Fig. 3 and Tables 1 and 2). After 18 months, soil organic matter recovered to concentrations comparable to the remaining treatments. Differences among the remaining treatments were small and varied throughout the sampling periods. Total soil N was strongly related to soil carbon (R^2= 0.93); thus, we expect patterns of total N differences among treatments to follow those for soil organic matter.

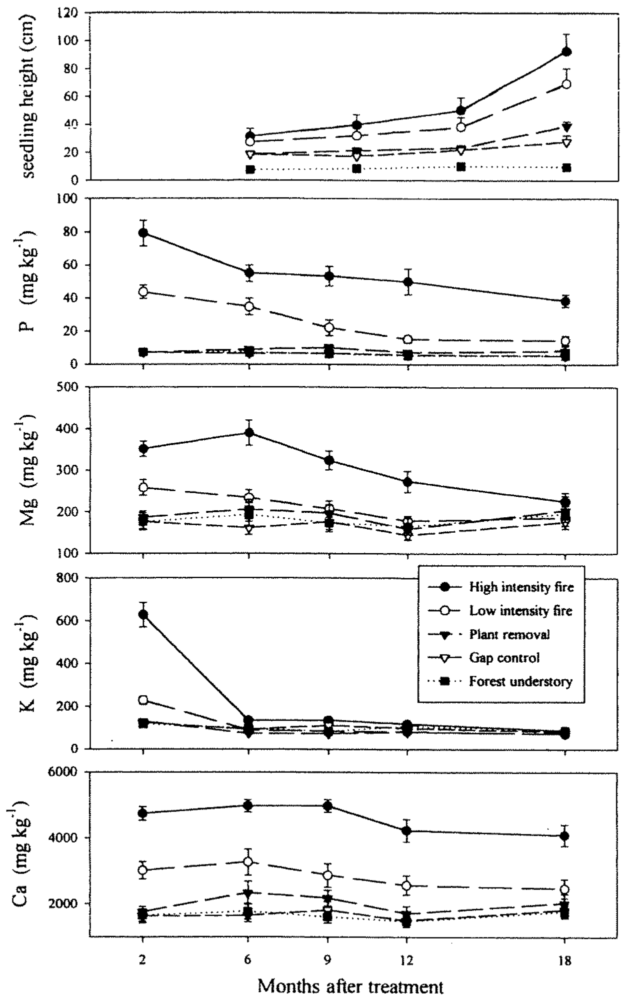

Figure 1. Seedling heights of *Anadenanthera colubrina*, and Mehlich-I extractable soil concentrations of P, Mg, Ca, and K in soil samples (0–8 cm depth) in four treatments and understory forest sites at five sampling times over an 18-month period following fires (bars = S.E., *n*=16).

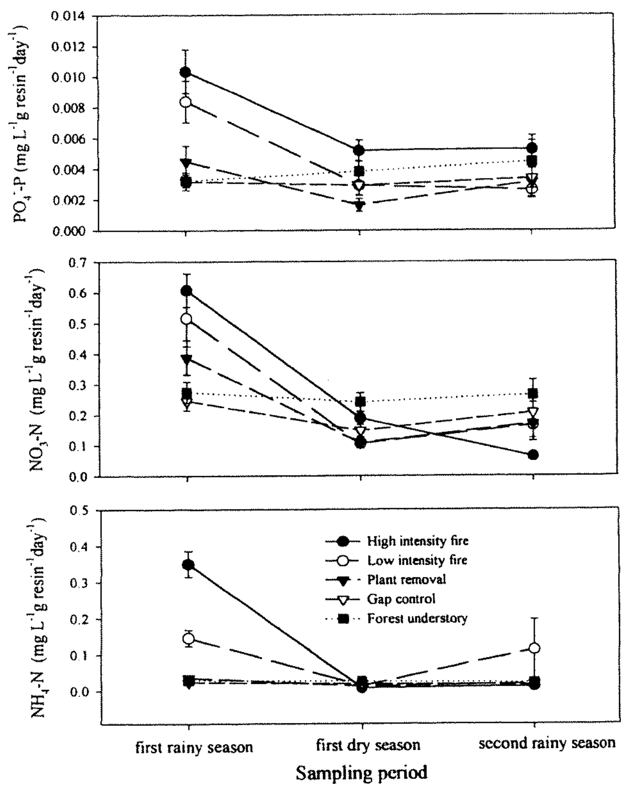

Figure 2. Resin-available ammonium, nitrate, and phosphate in four treatments and understory forest sites determined from exchange resins buried in soil at 5 cm depth during three periods following fires (bars = S.E., *n*=16). Resins were buried for approximately 3 months during each period. Time since fires of sampling periods were: first rainy season (2–5 months), first dry season (8–11 months), and second rainy season (15–18 months).

Although significant differences in soil water content were detected among treatments, differences were not large and patterns were not consistent over the sampling period (Fig. 3 and Tables 1 and 2). The forest understory plots had the lowest soil water content during the first 9 months, but this difference disappeared after 12 months. Larger differences in soil water content were due to seasonal changes.

Soil strength after high-intensity fires, initially the lowest among treatments, increased sharply during the first year (Fig. 3, Table 1). Water infiltration rates were significantly lower after high-intensity fires than other treatments ($F = 31$, $P < 0.001$; Fig. 4). Bulk density after high-intensity fires was significantly greater than in forest plots after 6 and 12 months ($F = 3.1$, $P = 0.02$, $n = 10$). There were no significant differences among the remaining treatments.

Treatment effects on seedling height

Seedlings in high- and low-intensity fire treatments were significantly taller than seedlings in the gap control or forest understory; seedling height in the plant removal treatment was intermediate ($F = 15.4$, $P < 0.001$, Fig. 1).

Discussion

Effects of high-intensity fire on soil properties

High intensity fires caused significant changes in both soil chemical and physical properties; increases in available nutrients were coupled with losses of soil organic matter, total soil nitrogen, and altered soil structure.

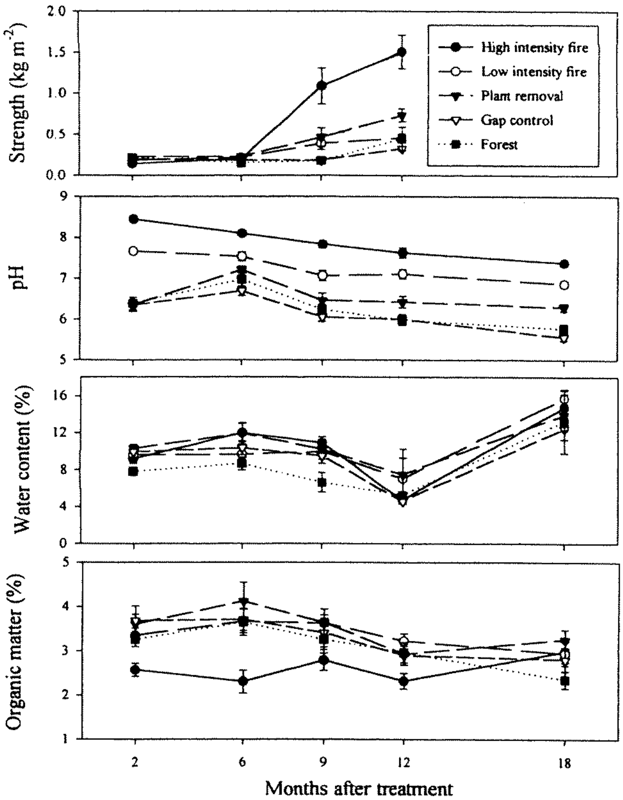

Figure 3. Soil pH, air-dry water content, and organic matter content measured in soil (0–8 cm depth) in the four treatments and understory forest sites at five sampling times over an 18-month period following burns. Soil strength was measured at the soil surface with a soil penetrometer at four sampling periods over a 12-month period following burns. Water content is expressed as percent of air-dry weight (bars = S.E., n=16).

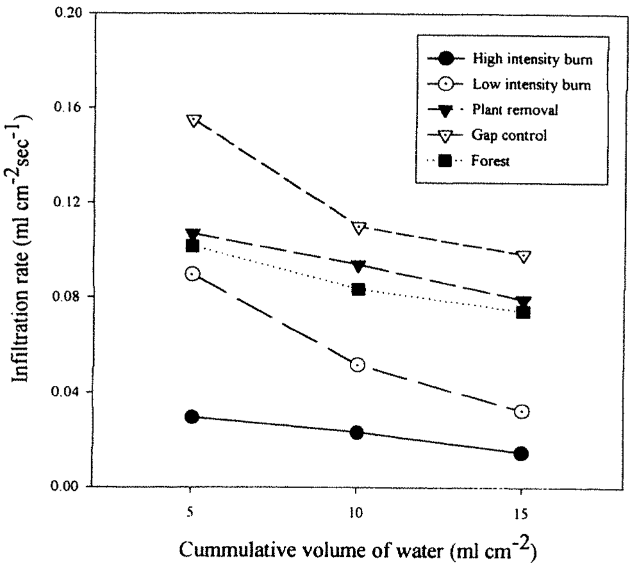

Figure 4. Water infiltration rates of soil in four treatments and forest understory sites. Infiltration was measured as the time required for the first 5 ml of a 10-ml column of water to infiltrate soil (n=4).

The large amount of ash deposited following high-intensity fires was likely the major contributor of increased soil pH and increased soil concentrations of extractable Ca, K, Mg and P. We estimated the masses of cations and P deposited in ash to be: 524 g/m^2 of Ca, 83 g/m^2 of K, 26 g/m^2 of Mg, and 7.7 g/m^2 of P. Soil heating may also have increased extractable Ca, K, Mg, and P through mineralization of organic forms (Giovannini et al., 1990), however this pathway was likely less important than contributions from ash. Inorganic P additions in ash were also likely the largest cause of increases in resin-available PO_4^{-3}-P. Rice (1993) found that soil PO_4^{-3}-P concentrations in Californian chaparral following fire were correlated with ash depth rather than fire intensity.

Increased resin-available nitrogen (NH_4^+-N and NO_3^--N) after high-intensity fires is attributed to the mineralization of organic forms of nitrogen found in soil organic matter and unburned slash fragments. Due to nitrogen's low temperature of volatilization (200°C; Weast, 1988), its concentration in ash was likely negligible. Increased NH_4^+-N following fires was probably enhanced by soil microbial death, which occurs at temperatures as low as 50–121°C (Neary et al., 1999). Similarly, Matson et al. (1987) attributed increases in net nitrogen mineralization to microbial death following slash and burn on volcanic soils in Costa Rica. Increased NO_3^--N concentrations were likely caused by increased nitrification rates following fires. Fire generally creates favorable conditions for nitrification by raising pH values and base saturation (Pritchett and Fisher, 1987). Both Matson et al. (1987) and Montagnini and Buschbacher (1989) attributed increased nitrate concentrations to enhanced nitrification rates following slash and burn in Costa Rica and Venezuela, respectively.

An important feature of the increase in resource availability produced by fire is the transient nature of the increases. Within 8 months of fires (after the first rainy season), inorganic N declined to levels found in adjacent forest. Decreases in cation concentrations over the 18-month post-fire period correspond with their mobility and susceptibility to leaching (K>Mg>Ca).

The net loss of soil organic matter caused by high-intensity fires was predictable based on the high soil temperatures measured during fires. Soil organic matter loss is a direct effect of soil heating; distillation of volatile organic compounds occurs between soil temperatures of 100–300°C and near complete loss of soil organic matter at temperatures >450°C (Giovannini et al., 1990; Hosking, 1938). Decreases in soil organic matter are often reported following the intense fires typical of slash burning in the tropics (Rab, 1996; Mackensen et al., 1996; Uhl and Jordan, 1984). The recovery of soil organic matter during the second year following fires may have been due to decomposition of fine roots and litter from colonizing vegetation, although the rate of recovery is notably high and faster than anticipated.

Due to its low temperature of volatilization, patterns of total soil N loss is closely linked to the consumption of soil organic matter; thus, we expect the loss of total soil N during high-intensity fires approximates the loss of soil organic matter (~loss of 28%). Decreases in total soil N are reported following slash burning in the tropics (Costa Rica: Ewel et al., 1981; Venezuelan Amazon: Uhl and Jordan, 1984).

The decrease in soil organic matter caused by high-intensity fires likely influenced the substantial changes in soil strength, bulk density, and water infiltration rates. The increase in surface soil strength during the first year following high-intensity fires was likely due to the settling of soil minerals and ash into spaces left void by organic matter and fine roots. This settling of soil particles would also contribute to greater soil bulk densities. Decreased macro-pore space would explain the lower infiltration rates observed in this treatment.

It was expected that high-intensity fires would result in lower soil water contents than other gap treatments. Decreased soil organic matter content lowers soil water holding capacity, decreased albedo due to a blackened soil surface plus exposure can increase water evaporation from soil, and slowed infiltration rates can increase surface run-off. In this study however, soil water contents were not significantly lower after high-intensity fires than other treatments. The predicted changes may have been offset by reduced transpiration in high-intensity burn plots, where total vegetative cover recovered more slowly than in other treatments (Kennard, 2000). Also, the lowered infiltration rates after high-intensity fires likely did not result in surface runoff: the lowest infiltration rate recorded in a high-intensity burn plot was 5 times faster than the rate needed to absorb a 5 cm h^{-1} rainfall (0.002 cm^3 cm^{-2} s^{-1}).

Effects of low-intensity fires on soil chemical and physical properties

We attribute the increases in soil pH, and extractable P, Ca, Mg, and K concentrations after low-intensity fires to the release of these basic cations from soil organic matter during soil heating, as very little ash was deposited during this treatment. Low-intensity fires increased resin-available N levels, although to a lesser degree than high-intensity fires. Temperate zone studies have noted that soil inorganic N increases as fire intensity increases from low to moderate levels (Dunn and DeBano, 1977; Giovannini et al., 1990; Kutiel et al., 1990; McMurtrie and Dewar, 1997; Rice, 1993; Weston and Attiwill, 1996).

Average surface temperatures during low-intensity fires (160°C) were not high enough for the consumption of soil organic matter, as reflected by organic matter contents of soil sampled from this treatment. In fact, average soil organic matter contents after low-intensity fires were greater than those of adjacent forest soils. Increases in soil organic matter have been shown to occur during light to moderate fires due to the incorporation of unburned or partially burned slash fragments into soil (Hungerford et al., 1990; Stromgaard 1992).

Soil strength, bulk density, water infiltration, and water repellency following low-intensity fires were not different from those in unburned treatments. Again, this pattern may reflect the influence of organic matter on soil physical characteristics.

Effects of plant removal and canopy gap formation on soil chemical and physical properties

Soil moisture content was greater in all of the gap treatments than forest plots for the first 9 months following fires. This difference, likely due to decreased transpiration (Vitousek and Denslow, 1986), diminished over the first year as the amount of vegetation in gaps increased.

Other than the observed differences in soil moisture contents, plant removal and gap treatments did not significantly change soil chemical or physical properties from those in adjacent intact forest. Although it is hypothesized that the increased soil temperatures, moisture, and litter depth in tree fall gaps will increase nutrient availability (Bazzaz, 1980), conclusive evidence to suggest this is true has not been reported (Luizao et al., 1998; Vitousek and Denslow, 1986).

Most of the variation observed within the plant removal, gap control, and forest plots over time was due to seasonal changes. Soil moisture content varied predictably with changes in rainfall and NO_3^- availability declined slightly during the dry season. This observation agrees with the few studies of nutrient cycling conducted in tropical dry forests which have shown that nitrification rates are highest during the rainy season and lowest at the end of the dry season (Garcia-Mendez et al., 1991; Singh et al., 1989; see also Smith et al., 1998).

Effects of treatments on tree seedling growth

Despite the potentially negative effects of increased bulk density and soil strength, lowered water infiltration rates, and possibly toxic effects of cations on plant growth, seedling heights of *A. colubrina* were greatest following high-intensity fires. This increased growth in intensely burned soils may be due to several factors. Initially, soil strength in high-intensity fire plots was the lowest of all treatments, therefore early colonizing seedlings should not have experienced mechanical impedance of root growth. Secondly, nutrient concentrations were highest following high-intensity fires, which may have offset decreased movement of nutrients in water through the soil. Also, toxic levels of cations may only have been a factor in small areas of high ash deposition or severely scorched soils; seedlings may not have been able to establish in these small areas and, therefore, the effects on growth were not observed. Most importantly, the density of plants colonizing after high-intensity fires was low, so that established tree seedlings likely benefited from reduced competition for soil water and nutrients.

Although seedlings that established soon after fires benefited from greater resource availability, the effects of high-intensity fires on tree seedling growth may not be as beneficial in subsequent years. Due to the decrease in nutrient availability during the first year following burns, seedlings establishing in following years may show the effects of degraded soil structure. As soil structure can take years to decades to recover, prescribed burns of low to medium intensity, which can increase nutrient availability without damaging soil, may be the best option in the long term.

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