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Persistence of tree related patterns in soil nutrients following slash-and-burn disturbance in the tropics

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Abstract

Individual trees are known to influence soil chemical properties, creating spatial patterns that vary with distance from the stem. The influence of trees on soil chemical properties is commonly viewed as the agronomic basis for low-input agroforestry and shifting cultivation practices, and as an important source of spatial heterogeneity in forest soils. Few studies, however, have examined the persistence of the effects of trees on soil after the pathways responsible for the effects are removed. Here, we present evidence from a Mexican dry forest indicating that stem-related patterns of soil nutrients do persist following slash-and-burn removal of trees and two years of cropping. Pre-disturbance concentrations of resin extractable phosphorus (P), bicarbonate extractable P, NaOH extractable P, total P, total nitrogen (N) and carbon (C), KCl extractable nitrate (NO_3^-), and net N mineralization and nitrification rates were higher in stem than dripline soils under two canopy dominant species of large-stemmed trees with contrasting morphologies and phenologies (*Caesalpinia eriostachys* Benth. and *Forchhammeria pallida* Liebm.). These stem effects persisted through slash burning and a first growing season for labile inorganic and organic P, NaOH inorganic P, and plant-available P, and through a second growing season for labile organic P, NaOH organic P, and plant-available P. While stem effects for extractable NO_3^-, net nitrification rates, total N and C disappeared after felling and slash burning, these stem effects returned after the first growing season. These results support the view that tree-influenced patterns of soil nutrients do persist after tree death, and that trees contribute to the long-term spatial heterogeneity of forest soils.

Introduction

The influence of trees on soil has been widely recognized in mixed forests and mono-specific stands in temperate regions (Zinke and Crocker, 1962; Tiedemann and Klemmedson, 1973; Everett et al., 1986; Boettcher and Kalisz, 1990; Andersson, 1991; Bellot and Escarre, 1991; Klemmedson and Wienhold, 1992; Binkley 1996), in association with agroforestry techniques (Leite and Valle, 1990; Drechsel et al., 1991; Rhoades, 1995; Binkley, 1997; Binkley and Giardina, 1997; Rhoades, 1997), in tropical savannas (Kellman, 1979; Belsky et al., 1989; Weltzin and Coughenour, 1990; Isichei and Muoghalu, 1992; Vetaas, 1992; Mordelet et al., 1993; Belsky, 1994), and to a lesser extent in natural closed canopy moist forests of tropical regions (Rhoades et al., 1994). The extent to which trees influence soil depends upon the tree species and environment in question, and the nutrient being measured (Zinke, 1962; Ko and Reich, 1993; Koch and Matzner, 1993). In stand studies, tree influences are sometimes species specific (Drechsel et al., 1991; Son and Gower, 1992; Montagnini and Sancho, 1994; Giardina et al., 1995; Ewers et al., 1996; Binkley and Giardina, 1997; Compton and Cole, 1998).

The influence of trees on soil is directly relevant to low-input shifting cultivation or agroforestry systems, for which trees are the primary source of increased

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soil fertility (Rhoades, 1997). While substantial effort has been directed towards understanding how these influences develop, relatively little is known about how long these single tree stem effects persist after the pathways that created the effects are removed. Such information could be useful in gauging the sustainability of tree-based agroforestry practices. Additionally, because disturbance is a natural component of most forests, and heterogeneity of soil nutrients is an obstacle to growing plants (Jenny, 1941; Caldwell, 1994; Grime, 1994; Stark, 1994), information on the persistence of such influences following disturbance could be useful to efforts that seek to model patterns of plant growth in natural systems.

To establish whether stem-related patterns existed at our tropical dry forest research site, we measured anion exchange resin extractable P, bicarbonate extractable P, NaOH extractable P, total P, KCl extractable ammonium (NH_4^+) and NO_3^-, net N mineralization and nitrification rates, and total N and C in pre-disturbance soils near tree stems and outside the canopy dripline of large-stemmed *C. eriostachys* and *F. pallida* individuals. The two tree species used in our study were selected because differences in tree morphology, phenology, litter quality, and litter quantity were expected to correspond to differences in the size of their influence on the soil properties measured. For both species, concentrations of these nutrients were higher in stem than dripline soils. The specific mechanisms responsible for the pre-disturbance patterns in soil nutrients were not examined. However, the presence of stem-related gradients in soil nutrients was a prerequisite for testing the following hypotheses: (1) slash burning would eliminate most or all stem- and/or species-related effects initially measured for plant-available soil P and N, and total soil P, N, and C; (2) if stem- and/or species-related effects did persist through burning, then cropping and harvesting, establishment of pasture, and cattle introduction to the site, would eliminate these remaining effects. The conversion of dry forest to active pasture is a severe, multi-step disturbance that involves cutting under-story vegetation, felling of trees early in the dry season, burning forest slash at the end of the dry season, planting crops with the onset of rain, harvesting crops, and later pasture establishment and grazing (Maass et al., 1988). Therefore, examining the persistence of stem-related patterns in soil nutrients in this context provides a robust test of the broader hypothesis that trees increase the long-term heterogeneity of soil nutrients (Jenny, 1941; Stark, 1994).

A Mexican tropical dry forest site was selected to test these hypotheses for several reasons. Dry forest is geographically the most extensive forest type in the tropics, comprising ~42% of all tropical forest cover (Murphy and Lugo, 1986). Dry forests are considered to be among the most endangered of tropical ecosystems (Janzen, 1988), in large part because they support the highest densities and largest numbers of people in the tropics (Murphy and Lugo, 1986). Also important, relative to other forest types in the tropics, little is known about how dry forests respond to disturbance (Kauffman et al., 1993; Giardina et al., 1999).

Methods

Study area

The study was conducted on a prominent north-south ridge east of the Ejido San Mateo (19°31′ N, 105°06′ W), approximately 10 km north of the Chamela Biological Station (Institute of Biology at the National Autonomous University of Mexico), in the state of Jalisco on the Pacific coast of Mexico. This dry, deciduous closed canopy forest receives approximately 80% of its 750 mm mean annual precipitation (± 119 mm) between July and October (Bullock 1986). Mean annual temperature is 24.9 °C, with monthly averages ranging from 20 °C in January to 27 °C in August (Bullock, 1986). The region consists of low rolling hills. Elevation at the study site is approximately 200 m and slopes range from 0 to 35 degrees. The soils (isohyperthermic Typic Ustorthents) are shallow (<1 m), sandy loam in texture, and derived from a rhyolitic parent material which is low in P (Maass et al., 1988). Soil pH ranges from 6.0–7.0 (Maass et al., 1988). Leaf flush for most species begins with the onset of the rainy season in late June or early July (Bullock and Solis-Magallanes, 1990), suggesting that water availability limits growth during the dry periods. Initial studies on P use efficiencies, P retranslocation rates, and tree responses to in-field P fertilization indicate that during the rainy season P is limiting to plant growth in the region of this study (Jaramillo and Sanford, 1995).

Prior to conversion, the study site was classified as ‘tropical deciduous forest’ (Rzedowski, 1978). Because of the tremendous diversity of flowering plants, which includes some 6,000 species (Toledo and Ordonez, 1993) of which 70% are endemic to Mexico (Rzedowski, 1993), this forest type is part of the

second most important biological zone in Mexico. In upland sites at the nearby Chamela Biological Station there are nearly 800 herbaceous and arboreal species in 107 families (Lott 1985), with an average of 30 tree species $\geq$ 0.1 m in diameter at breast height (DBH) per 0.1 ha (Lott et al., 1987). The most common families in the area of this study are Leguminosae, Euphorbiaceae, and Rubiaceae.

Two contrasting canopy tree species were examined in this study: *Caesalpinia eriostachys* Benth. (Leguminosae) and *Forchhammeria pallida* Liebm. (Capparidaceae). The non-nitrogen fixing legume, *C. eriostachys*, is a monoecious canopy dominant that grows to 12 m. *C. eriostachys* is one of the most common tree species in the region (Lott et al., 1987; Bullock and Solis-Magallanes, 1990; Martinez-Yrizar and Sarukhan, 1990), and at two nearby sites *C. eriostachys* was among the largest producers of litter per unit area (Cook, 1983). Senescent leaves of *C. eriostachys* have been shown to decompose more rapidly than litter fall of other species in the region (Martinez-Yrizar, 1984). This legume also has an irregular, perforated stem or multiple stems that provides an extensive surface for stemflow leaching. *Forchhammeria pallida* is a common, dioecious tree, 3–10 m tall with small canopy extent (Hendricks, 1990). Unlike most dry forest trees, *F. pallida* begins leaf flush at the onset of the dry season and loses its leaves during the rainy season, hence the description wet deciduous (Fanjul and Barradas, 1987). *Caesalpinia eriostachys* is a tall, large-stemmed, and spreading crown tree, while *F. pallida* is a tall, thin-stemmed, and narrow crown tree; both were abundant in the study area. Other common canopy species in the study area included *Lysiloma microphylla* Benth. (Leguminosae), *Bernardia spongiosa* McVaugh (Euphorbiaceae), and *Pithecellobium mangense* (Jacq.) MacBride (Leguminosae) (D. Roth, personal communication).

The conversion of dry forest to active pasture involves cutting of the under story vegetation with machetes and felling trees early in the dry season (March). In May, forest slash is burned, and crops and pasture grasses are planted with the onset of rains in June. Crops are harvested in September and October. Pasture is established for $\sim$1 yr, after which cattle are introduced to pasture for grazing (Maass et al., 1988). This form of land use is the primary cause of lost forest cover in the region (Maass et al., 1994).

Field sampling

Three ha of intact closed canopy forest (>100 yr) were converted to crops and then pasture by traditional slash-and-burn methods; wood was not harvested prior to burning slash. Ten large-stemmed individuals each of *C. eriostachys* and *F. pallida* (Figure 1) were identified in the three ha area. Prior to forest cutting, each individual tree was marked with permanent metal stakes, tagged, and mapped. Canopy area was calculated for each tree using the mean of four radii measured in the principle directions from the tree stem to the edge of the canopy. Tree height, basal diameter, and percent slope were also measured.

Soils were sampled at randomly selected locations adjacent to the tree stem and at the canopy dripline from 0–0.02 m and 0.02–0.10 m depths. Adjacent to trees, soils were sampled 0.05 to 0.15 m away from the stem; soils from the canopy dripline were sampled just beyond the canopy edge, but at least 1.0 m from any tree stem with a DBH > 0.1 m. Subsequent sampling was paired clockwise with the original pre-burn sample points. Soils for both tree species were sampled concurrently in: March, 1993, 3 d after cutting of the forest (pre-burn); May, 1993, 1 d after slash burning (post-burn); and, in December, 1993, at the end of the first growing season. Soils for *C. eriostachys* were also sampled in December, 1994, at the end of the second growing season. In December, 1994, 0-0.05 m depth soils from a single large-stemmed *C. eriostachys* individual in adjacent intact forest was sampled every 0.5 m along a north and south transect (cross-slope), from the tree stem to 0.1 m beyond the dripline. Prior to all sampling, soils were cleaned of either forest floor material (pre-burn), ash (post-burn), or litter (post-growing season 1 and 2). All soils were air dried and sieved to 2 mm prior to analyses.

Pyrometers were used to measure soil temperatures during slash burning to a depth of $\sim$0.055 m (Fenner and Bentley, 1960). Temperature sensitive paints were applied to 0.05×0.08 m mica sheets backed by insulating material. The paints had melting points of 59, 104, 204, 316, 538 and 816 °C. Pyrometers were placed at 12 stratified points in the soil prior to burning with no relation to tree location and collected 24 hr after burning. The mean belowground depth for each melting point was then calculated.

Laboratory analyses

A modified sequential P fractionation technique (Hedley et al., 1982) was used to separate soil P into

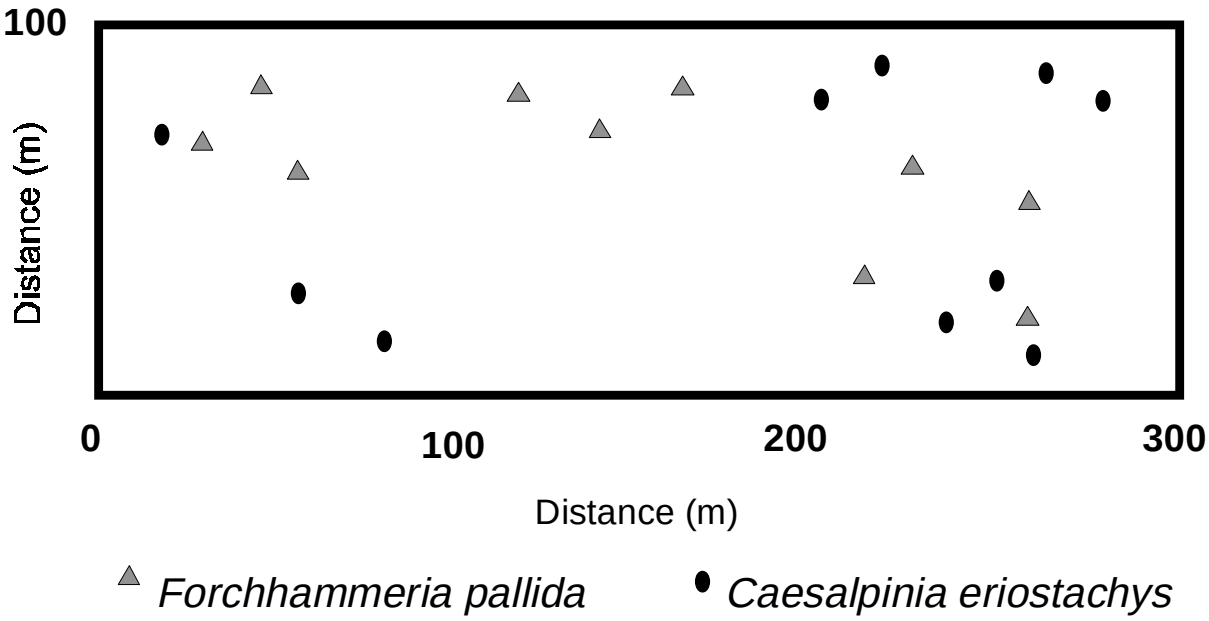

Figure 1. Distribution of *Forchhammeria pallida* (n = 10) and *Caesalpinia eriostachys* (n = 10) individuals in the 100 m × 300 m research site.

fractions that vary in availability for plant growth. For three treatment periods, soils from both depths and both locations were fractionated for the ten individuals of each tree species (3 treatments×2 soil depths×2 sample locations×10 individual trees×2 species for a total of 240 samples), and for the second growing season, only soils from *C. eriostachys* were fractionated (2 depths×2 locations×10 trees for a total of 40 samples). One g of air dried soil was sequentially extracted with: a 10×60 mm Ionics brand anion exchange resin strip in deionized water; followed by a 0.5 *M* sodium bicarbonate ($NaHCO_3$) solution buffered to pH 8.5; and, finally a 0.2 *M* sodium hydroxide (NaOH) solution. Total P (organic + inorganic) in the $NaHCO_3$ and NaOH extracts was determined by acidified ammonium persulfate digestion. Inorganic P (Pi) was measured directly and organic P (Po) was calculated as the difference between total P and Pi. All P extracts were colorimetrically analyzed on a Lachat Instruments *QuikChem* AE Ion Analyzer according to method 10-115-01-1-B (1992). Anion exchange resins remove solution Pi, the most plant-available Pi form in soil. $NaHCO_3$ extractable Po and Pi is thought to represent easily solubilized Pi adsorbed to soil surfaces and readily mineralized Po. NaOH extractable Pi is thought to represent moderately-available Pi in microbial biomass and chemisorbed to iron and aluminum surfaces in soil; NaOH extractable Po represents moderately-available Po that is held as microbial and soil organic matter Po. The resin Pi and $NaHCO_3$ Pi fractions were combined and designated as labile Pi. The resin, $NaHCO_3$, and NaOH P fractions were combined and designated as plant-available P (Hedley et al., 1982). Separate sub-samples of soil were analyzed for total soil P by NaOH fusion in heated nickel crucibles (Smith and Bain, 1982). Non-plant-available P was then calculated as the difference between total P and plant-available P.

Total soil C and N were determined by dry combustion on a LECO-1000 CNH analyzer. For three treatment periods, total soil C and N analyses were performed on the 0–0.02 m depth soils for both locations for six randomly selected individuals of each tree species (3 treatments×2 locations×6 trees×2 species for a total of 72 samples).

For three treatment periods, mineral N was extracted from both depths and locations for the ten individuals of *C. eriostachys* only (3 treatments×2 depths ×2 locations×10 trees for a total of 120 samples). Aerobic incubations of mineral soil were used to measure net N mineralization and nitrification rates. Ten g fresh weight of each soil were incubated in plastic containers with loose fitting caps at 30 °C for 30 d at field capacity. Soil moisture content was periodically adjusted with deionized water to original field capacity. Ten g soil samples were shaken for 1 hr in 100 mL of 2 *M* potassium chloride (KCl) solution to extract soil ammonium (NH_4^+) and nitrate (NO_3^-) from a

set of soils prior to the incubation and on incubated soils (Keeney and Nelson, 1982). Samples were analyzed for $NH_4^+$and NO_3^- on a Lachat Instruments *QuikChem* AE Ion Analyzer according to methods 12-107-06-2-A (1990) and 12-107-04-1-B (1992), respectively. Net N transformations were calculated as follows (Hart et al., 1994): net mineralization = (NH_4-N + NO_3-N)t_1 - (NH_4-N + NO_3-N)t_0 and net nitrification = (NO_3-N)t_1 − (NO_3-N)t_0.

Bulk density was determined using a core method with a 0.05 m diameter ring (Blake and Hartge, 1986) for soils to a depth of 0–0.05 m. Soil density was based on 2 mm sieved oven dry weight. Bulk density cores were taken at stem and dripline locations for 10 individuals of each tree species in adjacent intact forest in May, 1994, and in the three ha treatment site in December, 1994 (2 locations×10 trees×2 species for a total of 40 samples). Bulk densities were used to convert 0–0.02 m depth pre-burn and PG2 soil P, C and N concentrations to a g m^{-2} basis. All soil P, C, and N measures are presented on an oven dry basis, with soil moisture content determined following oven drying for 24 hr at 105 °C. Soil pH of 0-0.02 m depth soils (McLean, 1982) was measured with a glass electrode in a well mixed 2:1 solution of deionized water and soil.

Statistical analyses

Two-way analysis of variance (ANOVA) for a split-plot design was used to compare soil P fractions, bulk density, pH, and total P, N, and C. In this design, each tree represented a plot split into stem and dripline treatments with one sample taken per treatment (Wilkinson, 1990). The main effect was 'species', 'individual trees' were used as plot effects, and 'location'-within-trees were a split-plot effect. The error term for the main effect was plot-within-species sum of squares. The error for the location (= split-plot) effect and the species×location interaction was the sums of squares for the location×plot-within-species. Each depth and each treatment period were analyzed separately. There were no significant species by location interactions in the ANOVA analyses. A Student's *t*-test, using a pooled variance estimate, was used to compare tree basal diameter, tree height, tree canopy area and hill-slope angle of *C. eriostachys* and *F. pallida* (Wilkinson, 1990). A paired *t*-test was used to compare stem and dripline N concentrations for soils sampled from under *C. eriostachys* for each sampling period, and stem and dripline P fractions for soils sampled from under *C. eriostachys* for PG2 (Wilkinson, 1990). A paired *t*-test was also used to compare stem and dripline non-plant-available P and total P concentrations for *C. eriostachys* for the 0.02-0.10 m soil depth. Probability of a type I error of 0.05 was used in all comparisons.

Results

Pre-burn stem effects

Mean soil bulk densities at stem and dripline locations were 600 and 690 kg m^{-3} for *C. eriostachys* and 760 and 830 kg m^{-3} for *F. pallida*, respectively. The differences between stem and dripline soils were not significant. Mean soil pH for the 0–0.02 m soil depth ranged between 6.8–7.2 (Table 1), with no significant differences among locations and species.

All P fraction concentrations were significantly higher in stem than dripline soils at both depths and for both species (Tables 2 and 3). Concentrations of plant-available P (the sum of the individual Po and Pi

Table 1. pH of 0–0.02 m depth soils. Two-way ANOVA split plot analyses were used to make comparisons between species and between stem and dripline soils. Comparisons were not made between treatment periods. (n = 5)

Treatment	Location	pH	
		C. eriostachys	*F. pallida*
Pre-burn			
	stem	6.8 a	7.0 a
		(0.1)	(0.2)
	dripline	6.9 a	7.2 a
		(0.1)	(0.1)
Post-burn			
	stem	8.9 a	8.6 a
		(0.2)	(0.1)
	dripline	7.9 b	7.8 b
		(0.2)	(0.4)
Post-growing season 1	stem	7.8 a	7.8 a
		(0.1)	(0.1)
	dripline	8.0 a	7.9 a
		(0.1)	(0.1)

Note: Values are means with standard errors in parentheses. Means followed by different letters denote a significant difference at $P < 0.05$. Pair-wise comparisons are only for rows and columns within treatment periods.

Table 2. Plant-available phosphorus fractions extracted from 0–0.02 m depth soils. Two-way ANOVA split plot analyses were used to make comparisons between species and between stem and dripline soils for each phosphorus fraction. A paired *t*-test was used to make post-growing season 2 comparisons between stem and dripline soils for *C. eriostachys*. Comparisons were not made between treatment periods. (n = 10)

Treatment	Location	Plant-available phosphorus fractions (μg P g^{-1} soil) 0–0.02 m soil depth							
		Labile Pi		Labile Po		NaOH Pi		NaOH Po	
		C. eriostachys	*F. pallida*	*C. eriostachys*	*F. pallida*	*C. eriostachys*	*F. pallida*	*C. eriostachys*	*F. pallida*
Pre-burn									
	stem	63.9 a	70.7 a	24.7 a	32.2 b	36.4 a	35.9 a	179.7 a	194.8 a
		(7.2)	(15.5)	(2.1)	(3.0)	(2.6)	(4.1)	(11.3)	(21.2)
	dripline	30.7 b	31.8 b	13.2 c	23.5 d	28.4 b	26.6 b	127.9 b	158.3 b
		(3.7)	(2.4)	(1.5)	(1.7)	(2.7)	(2.0)	(8.1)	(18.7)
Post-burn									
	stem	331.0 a	420.9 a	21.3 a	29.1 b	110.2 a	122.9 a	74.1 a	65.6 a
		(50.6)	(57.1)	(3.2)	(2.8)	(19.8)	(33.1)	(15.0)	(9.0)
	dripline	191.7 b	250.0 b	19.2 a	29.6 b	59.3 b	73.3 b	74.5 a	89.2 a
		(38.4)	(51.0)	(1.3)	(3.1)	(15.2)	(20.6)	(9.0)	(19.5)
Post-growing season 1									
	stem	238.3 a	346.8 a	16.5 a	18.1 a	85.0 a	144.8 a	78.3 a	64.4 a
		(42.6)	(82.7)	(2.2)	(2.0)	(12.1)	(36.4)	(13.4)	(8.1)
	dripline	117.9 b	220.4 b	13.2 a	15.2 a	59.5 b	90.8 b	86.0 a	73.0 a
		(28.4)	(60.3)	(1.1)	(1.9)	(10.3)	(17.2)	(7.3)	(9.4)
Post-growing season 2									
	stem	145.9 a		17.3 a		55.0 a		143.4 a	
		(39.5)		(1.3)		(15.0)		(20.3)	
	dripline	106.9 a		12.8 b		58.2 a		86.8 b	
		(22.2)		(1.7)		(9.5)		(11.0)	

Note: Values are means with standard errors in parentheses. Means followed by different letters denote a significant difference at $P < 0.05$. Pair-wise comparisons are only for rows and columns within treatment periods.

fractions) and total P were also significantly higher in stem than dripline soils at both depths and for both species (Tables 4 and 5). When expressed on an area basis (g m^{-2}), concentrations of all P fractions and plant-available P were significantly higher in stem than dripline soils in 0-0.02 m depth soils of both species (Tables 6 and 7). All measures of pre-burn soil P from the north and south transect through a single large-stemmed *C. eriostachys* individual decreased with increasing distance from the tree stem (Figure 2a-c).

For *C. eriostachys*, net N mineralization rates were significantly higher at stem locations for 0.02–0.10 m depth soils only. Concentrations of KCl extractable NO_3^- and net nitrification rates were significantly higher in stem than dripline soils at both depths (Tables 8 and 9). Both the concentration and area basis content (g m^{-2}) of total C and N were significantly higher in stem than dripline soils (Tables 10 and 11).

Post-burn stem effects

During burning of forest slash, pyrometers recorded maximum soil temperatures exceeding 816 °C in the top 0.005 m of soil, with temperatures of at least 204 °C occurring to a depth of 0.018 m. These soil temperatures are among the highest reported in soils for tropical slash fires (Giardina et al., 1999). Following slash burning, soil pH increased ∼1 unit at the dripline and ∼2 units at the stem, resulting in a significant post-burn difference between stem and dripline soil pH (Table 1).

Following biomass burning, the labile Pi fraction in 0–0.02 m depth soils increased 4 to 7 fold. For both soil depths, stem concentrations of labile Pi were sig-

Table 3. Plant-available phosphorus fractions extracted from 0.02–0.10 m depth soils. Two-way ANOVA split plot analyses were used to make comparisons between species and between stem and dripline soils for each phosphorus fraction. A paired *t*-test was used to make post-growing season 2 comparisons between stem and dripline soils for *C. eriostachys*. Comparisons were not made between treatment periods. (n = 10)

Treatment	Location	Plant-available phosphorus fractions (μg P g^{-1} soil) 0.02–0.10 m soil depth							
		Labile Pi		Labile Po		NaOH Pi		NaOH Po	
		C. eriostachys	*F. pallida*	*C. eriostachys*	*F. pallida*	*C. eriostachys*	*F. pallida*	*C. eriostachys*	*F. pallida*
Pre-burn									
	stem	36.2 a	48.1 a	17.2 a	27.3 b	29.2 a	36.4 a	153.4 a	185.7 a
		(4.8)	(11.2)	(1.6)	(2.1)	(3.4)	(5.7)	(9.0)	(23.6)
	dripline	12.5 b	17.2 b	9.8 c	18.2 d	17.6 b	20.5 b	112.0 b	155.4 b
		(2.3)	(2.0)	(0.8)	(1.9)	(2.2)	(2.5)	(9.0)	(16.2)
Post-burn									
	stem	175.7 a	191.3 a	23.0 a	38.4 b	41.0 a	57.4 a	85.5 a	136.6 b
		(41.8)	(60.9)	(2.3)	(5.6)	(8.4)	(18.2)	(14.5)	(13.9)
	dripline	66.7 b	104.6 b	16.1 c	23.6 d	26.0 a	33.0 a	77.7 a	120.2 b
		(25.5)	(40.1)	(1.8)	(1.7)	(5.2)	(6.6)	(8.2)	(17.6)
Post-growing season 1	stem	126.1 a	146.3 a	22.6 a	23.9 a	60.5 a	64.7 a	111.7 a	128.2 a
		(27.2)	(42.1)	(2.4)	(3.2)	(8.5)	(11.4)	(8.7)	(15.1)
	dripline	37.1 b	27.5 b	13.8 b	16.4 b	27.2 b	27.1 b	106.2 a	128.1 a
		(13.0)	(7.7)	(1.2)	(0.9)	(5.3)	(3.1)	(10.4)	(15.6)
Post-growing season 2	stem	62.7 a		15.1 a		45.7 a		143.2 a	
		(18.3)		(2.1)		(9.9)		(13.5)	
	dripline	41.1 a		11.0 a		31.9 a		113.8 a	
		(9.7)		(1.1)		(7.7)		(13.9)	

Note: Values are means with standard errors in parentheses. Means followed by different letters denote a significant difference at $P < 0.05$. Pairwise comparisons are only for rows and columns within treatment periods.

nificantly greater than dripline concentrations (Tables 2 and 3). For both species, the labile Po fraction in 0–0.02 m depth soils decreased slightly at the stem, but increased at the dripline; labile Po in 0.02–0.10 m depth soils increased at both locations. Concentrations of labile Po were significantly higher in stem than dripline soils for the 0.02–0.10 m depth only. Concentrations of NaOH Pi increased following burning, with a significant stem effect persisting in 0–0.02 m depth soils. Concentrations of NaOH Po decreased following burning, with larger losses near stems eliminating the pre-burn stem effect for this P fraction. Post-burn concentrations of plant-available P at both depths, and total P in 0-0.02 m depth soils remained significantly higher in stem than dripline soils (Tables 4 and 5).

After burning, concentrations of KCl extractable NH_4^+ increased 5 to 11 fold in soils under *C. eriostachys*. Differences between stem and dripline soils were not significant for either soil depth (Tables 8 and 9). Concentrations of KCl extractable NO_3^- were greatly reduced; NO_3^- concentrations were ~3 to 16 fold higher in pre-burn than post-burn soils. Substantially larger post-burn loss of NO_3^- from stem soils eliminated any significant differences between stem and dripline locations for both depths. Net nitrification rates decreased in soils near the stem, but increased in soils from the dripline. Consequently, the significant pre-burn differences between stem and dripline soils did not persist for either depth after slash burning. Significant differences in net N mineralization rates between stem and dripline soils at either depth also did not persist. Larger losses of C and N in stem than dripline soils eliminated significant pre-burn differences between stem and dripline soils (Table 10).

Table 4. Plant-available phosphorus (sum of all the soil phosphorus fractions), non-plant-available phosphorus (difference between total phosphorus and plant-available phosphorus), and total phosphorus extracted from 0–0.02 m depth soils. Two-way ANOVA split plot analyses were used to make comparisons between species and between stem and dripline soils for each phosphorus measure. A paired *t*-test was used to make post-growing season 2 comparisons between stem and dripline soils for *C. eriostachys*. Comparisons were not made between treatment periods. (n = 10)

Treatment	Location	Phosphorus summary (μg P g^{-1} soil) 0–0.02 m soil depth					
		Plant-available P		Non-plant-available P		Total P	
		C. eriostachys	*F. pallida*	*C. eriostachys*	*F. pallida*	*C. eriostachys*	*F. pallida*
Pre-burn							
	stem	305 a	334 a	413 a	675 b	718 a	1009 c
		(21)	(41)	(34)	(47)	(47)	(84)
	dripline	200 b	240 b	380 a	600 b	581 b	840 d
		(15)	(22)	(37)	(48)	(48)	(55)
Post-burn							
	stem	537 a	639 a	300 a	401 a	837 a	1040 a
		(60)	(85)	(41)	(47)	(81)	(112)
	dripline	345 b	442 b	288 a	370 a	633 b	812 b
		(48)	(62)	(33)	(44)	(67)	(75)
Post-growimg season 1	stem	418 a	574 a	345 a	568 b	763 a	1142 a
		(48)	(115)	(60)	(87)	(66)	(197)
	dripline	277 b	399 b	441 a	479 b	717 a	878 a
		(37)	(71)	(43)	(45)	(61)	(111)
Post-growing season 2	stem	362 a					
		(52)					
	dripline	265 b					
		(37)					

Note: Values are means with standard errors in parentheses. Means followed by different letters denote a significant difference at $P < 0.05$. Pair-wise comparisons are only for rows and columns within treatment periods.

Post-growing season 1 stem effects

Soil pH decreased ~1 unit at the stem, but remained unchanged at the dripline (Table 1). The labile Pi and Po fractions decreased following the first growing season. Changes in the NaOH P fractions were more variable. Significant differences between stem and dripline soils persisted at both depths for labile Pi, NaOH Pi, and plant-available P (Tables 2 through 5), while significant differences for labile Po persisted in 0.02–0.10 m depth soils (Table 3).

Concentrations of KCl extractable NH_4^+ decreased in soils under *C. eriostachys* at both sample locations for both depths; differences between stem and dripline soils were not significant (Tables 8 and 9). Concentrations of KCl extractable NO_3^- increased for all soils following the first growing season; concentrations were significantly higher in stem than dripline soils for 0.02–0.10 m depth soils only. In 0–0.02 m depth soils, net N mineralization rates were significantly higher in stem than dripline soils (Table 8). Net nitrification rates decreased in dripline soils, but remained unchanged in stem soils; as a result, nitrification rates were significantly higher in stem than dripline soils for both depths. Total C and N were significantly higher in stem than dripline soils (Table 10). Notably, statistically significant differences between stem and dripline soils for net N mineralization and nitrification rates, and total C and N represented the return of stem effects that had been eliminated during slash burning.

Table 5. Plant-available phosphorus (sum of all the soil phosphorus fractions), non-plant-available phosphorus (difference between total phosphorus and plant-available phosphorus), and total phosphorus extracted from 0.02–0.10 m depth soils. Two-way ANOVA split plot analyses were used to make comparisons between species and between stem and dripline soils for plant-available phosphorus. A paired *t*-test was used to make post-growing season 2, non-plant-available phosphorus, and total phosphorus comparisons between stem and dripline soils for *C. eriostachys*. Comparisons were not made between treatment periods. (n = 10)

Treatment	Location	Phosphorus summary (μg P g^{-1} soil) 0.02–0.10 m soil depth					
		Plant-available P		Non-plant-available P		TotaI P	
		C. eriostachys	*F. pallida*	*C. eriostachys*	*F pallida*	*C. eriostachys*	*F. pallida*
Pre-burn							
	stem	236 a	298 b	531 a		767 a	
		(15)	(41)	(35)		(44)	
	dripline	152 c	211 d	454 a		606 b	
		(13)	(18)	(49)		(61)	
Post-burn							
	stem	325 a	424 a	319 a		644 a	
		(43)	(89)	(55)		(77)	
	dripline	186 b	282 b	343 a		529 a	
		(28)	(44)	(34)		(52)	
Post-growing season 1	stem	321 a	363 a	326 a		647 a	
		(34)	(65)	(48)		(70)	
	dripline	184 b	199 b	390 a		574 a	
		(24)	(19)	(36)		(52)	
Post-growing season 2	stem	267 a					
		(27)					
	dripline	198 b					
		(19)					

Note: Values are means with standard errors in parentheses. Means followed by different letters denote a significant difference at $P < 0.05$. Pair-wise comparisons are only for rows and columns within treatment periods.

Post-growing season 2 stem effects

Only soils sampled from under *C. eriostachys* were analyzed following the second growing season. Mean soil bulk densities for stem and dripline locations were not significantly different (860 and 890 kg m^{-3}, respectively). In 0–0.02 m depth soils, concentrations of labile Po, NaOH Po, and plant-available P were significantly higher in stem than dripline soils (Tables 2 and 4). In 0.02–0.10 m depth soils, stem concentrations of plant-available P were higher than dripline values (Table 5). On an area basis (g m^{-2}), quantities of labile Po and plant-available P in 0-0.02 m depth soils were significantly higher in stem than dripline soils (Tables 6 and 7).

Pre-burn species effects

Mean basal diameter, canopy height, and canopy area were significantly larger for *C. eriostachys* than *F. pallida* (Table 12). Pre-burn bulk densities for stem and dripline soils under *F. pallida* were significantly higher than respective soils under *C. eriostachys*. Neither soil pH (Table 1), nor mean percent slope of the sites that the trees occupied (Table 12), differed significantly between the two species.

Concentrations of labile Po, non-plant-available P, and total P in 0-0.02 m depth soils were significantly higher in stem and dripline soils under *F. pallida* than in respective soils under *C. eriostachys* (Tables 2 and 4). Significant differences were also found for labile Po and plant-available P in 0.02–0.10 m depth soils

Table 6. Plant-available phosphorus fractions extracted from 0–0.02 m depth soils. Two-way ANOVA split plot analyses were used to make pre-burn comparisons between species and between stem and dripline soils for each phosphorus fraction. A paired *t*-test was used for post-growing season 2 comparisons between stem and dripline soils for *C. eriostachys*. Comparisons were not made between treatment periods. (n = 10)

Treatment	Location	Plant-available phosphorus fractions (g P m^{-2} soil) 0–0.02 m soil depth							
		Labile Pi		Labile Po		NaOH Pi		NaOH Po	
		C. eriostachys	*F. pallida*	*C. eriostachys*	*F. pallida*	*C. eriostachys*	*F. pallida*	*C. eriostachys*	*F. pallida*
Pre-burn									
	stem	0.77 a	1.07 a	0.30 a	0.49 b	0.44 a	0.55 a	2.16 a	2.96 b
		(0.09)	(0.24)	(0.03)	(0.05)	(0.03)	(0.06)	(0.14)	(0.32)
	dripline	0.42 b	0.53 b	0.18 c	0.39 d	0.40 b	0.44 b	1.77 c	2.63 d
		(0.05)	(0.04)	(0.02)	(0.03)	(0.04)	(0.03)	(0.11)	(0.31)
Post-growing season 2	stem	2.51 a		0.30 a		0.94 a		2.47 a	
		(0.68)		(0.02)		(0.26)		(0.35)	
	dripline	1.90 a		0.23 b		1.03 a		1.55 a	
		(0.40)		(0.03)		(0.17)		(0.20)	

Note: Values are means with standard errors in parentheses. Means followed by different letters denote a significant difference at $P < 0.05$. Pair-wise comparisons are only for rows and columns within treatment periods.

Table 7. Plant-available phosphorus (sum of all the soil phosphorus fractions), non-plant-available phosphorus (difference between total phosphorus and plant-available phosphorus), and total phosphorus extracted from 0–0.02 m depth soils. Two-way ANOVA split plot analyses were used to make pre-burn comparisons between species and between stem and dripline soils for each phosphorus measure. A paired *t*-test was used to make post-growing season 2 comparisons between stem and dripline soils for *C. eriostachys*. Comparisons were not made between treatment periods. (n = 10)

Treatment	Location	Phosphorus summary (g P m^{-2} soil) 0–0.02 m soil depth					
		Plant-available P		Non-plant-available P		Total P	
		C. eriostachys	*F. pallida*	*C. eriostachys*	*F. pallida*	*C. eriostachys*	*F. pallida*
Pre-burn							
	stem	3.7 a	5.1 b	5.0 a	10.3 b	8.6 a	15.3 b
		(0.2)	(0.6)	(0.4)	(0.7)	(0.6)	(1.3)
	dripline	2.8 c	4.0 d	5.3 a	10.0 b	8.0 a	14.0 b
		(0.2)	(0.4)	(0.5)	(0.8)	(0.7)	(0.9)
Post-growing season 2	stem	6.2 a					
		(0.9)					
	dripline	4.7 b					
		(0.7)					

Note: Values are means with standard errors in parentheses. Means followed by different letters denote a significant difference at P <0.05. Pair-wise comparisons are only for rows and columns within treatment periods.

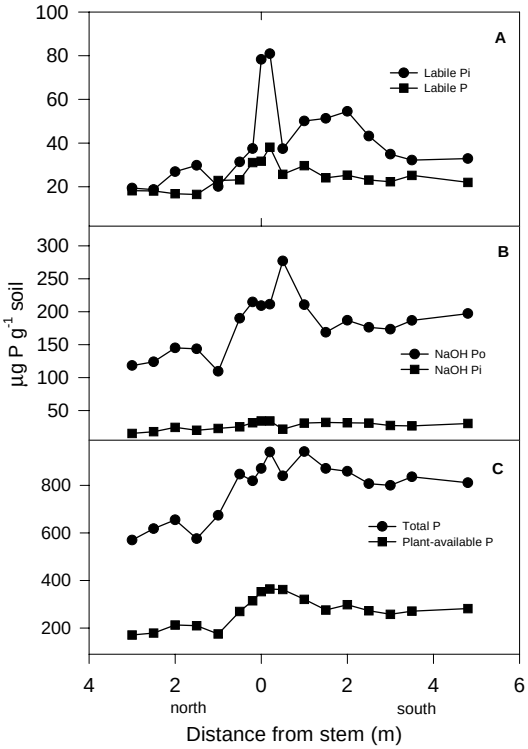

Figure 2. Soils sampled at 0–0.05 m depth every 0.5 m in two transects extending to the north and south of the stem of one individual *C. eriostachys* to 0.1 m beyond the dripline. Tree stem = 0 m, north dripline = 2.9 m, and south dripline = 4.7 m. (A), Labile inorganic and organic phosphorus fraction. (B), Sodium hydroxide extractable inorganic and organic phosphorus fraction. (C), Total phosphorus and plant-available phosphorus.

(Tables 3 and 5). There were no pre-burn species effects for total soil C or N (Table 10). On an area basis (g m^{-2}), quantities of labile Po, NaOH Po, plant-available P, non-plant-available P, total P, and total N in 0–0.02 m depth soils were significantly higher under *F. pallida* than *C. eriostachys* (Tables 6, 7 and 11).

Post-burn species effects

Following slash burning, the naturally perforated stems of *C. eriostachys* continued to smolder for days, with stems burning completely to the soil and leaving a ring of roots at the base; in several cases roots burned into the soil. In contrast, the stems of *F. pallida* remained relatively intact following the burn. These differences indicate that stem soil temperatures were likely higher and heating duration longer for *C. eriostachys*.

A species effect for labile Po persisted at both depths, with concentrations remaining significantly higher under *F. pallida* than *C. eriostachys* (Table 2). There was a first time appearance of a species effect for NaOH Po in 0.02-0.10 m depth soils (Table 3), and for total N in 0–0.02 m depth soils (Table 10) with nutrient concentrations significantly higher under *F. pallida*.

Post-growing season 1 species effects

After the first growing season, there were no significant differences between *C. eriostachys* and *F. pallida* for any measure of plant-available P or total C in soil. A significant species effect persisted in 0–0.02 m depth soils for non-plant-available P (Table 4) and total N (Table 10).

Discussion

Pre-burn stem effects

Several studies have documented that nutrient concentrations are higher near tree stems than beyond the canopy edge, and that gradients exist, extending outward from tree stem to dripline (Zinke, 1962; Zinke and Crocker, 1962; Kellman, 1979; Bernhard-Reversat, 1982; Everett et al., 1986; Belsky et al., 1989). In a Utah semi-desert shrub community, Charley and West (1975) found significantly higher concentrations of organic P and bicarbonate P in soils under bushes than in soils between bushes. In a west African savanna study, Mordelet et al. (1993) found significantly higher concentrations of available P under tree clumps than in open grassland. In contrast, a Nigerian savanna study documented no significant differences in plant-available P in soils from under trees or open grassland (Isichei and Muoghalu, 1992). Similarly, Tiedemann and Klemmedson (1973) found no significant differences in total P for soils from under mesquite trees or open areas, and Charley and West (1975) found only variable differences in total P for soils under bushes as compared to the spaces between bushes. A Kenyan savanna study documented significantly higher net N mineralization rates under savanna tree species than in the surrounding grasslands (Belsky et al., 1989). In a central Malawi study, net N mineralization rates were between 1.5 to 7 times higher under large tree canopies than in open sites (Rhoades, 1995). Several studies have documented significantly higher total soil N, C and/or soil microbial biomass-C in soils under trees or shrubs than in soils from open areas (Tiedemann and Klemmedson, 1973; Charley and West, 1975;

Table 8. Initial extractable ammonium and nitrate, and net N mineralization and nitrification rates in 0–0.02 m depth soils for *C. eriostachys*. A paired *t*-test was used to make comparisons between stem and dripline soils for each nitrogen measure. Comparisons were not made between treatment periods. (n= 10)

Treatment	Location	*Caesalpinia eriostachys* 0–0.02 m soil depth			
		Initial extractable (μg N g^{-1}) soil)		Transformation rates (μg N g^{-1} soil mo^{-1})	
		Ammonium	Nitrate	Net N mineralization	Net nitrification
Pre-burn					
	stem	17.6 a	63.2 a	128.5 a	144.7 a
		(3.6)	(16.8)	(12.8)	(12.6)
	dripline	12.1 a	18.0 b	93.0 a	103.8 b
		(2.4)	(5.1)	(13.3)	(13.3)
Post-burn					
	stem	100.1 a	3.7 a	52.0 a	95.1 a
		(17.8)	(2.9)	(21.5)	(25.5)
	dripline	111.9 a	5.2 a	62.3 a	124.9 a
		(17.6)	(2.0)	(14.9)	(22.4)
Post-growing season 1	stem	34.8 a	49.9 a	49.4 a	83.7 a
		(10.1)	(17.1)	(12.5)	(13.9)
	dripline	12.4 a	15.3 a	18.7 b	30.8 b
		(1.3)	(5.6)	(3.4)	(4.0)

Note: Data are means with standard errors in parentheses. Means followed by different letters denote a significant difference at $P < 0.05$. Pair-wise comparisons are only for columns within treatment periods.

Belsky et al., 1989; Isichei and Muoghalu, 1992; Ko and Reich, 1993; Mordelet et al., 1993; Alpert and Mooney, 1996).

Several hypotheses have been proposed to explain the apparent influence of trees on soil (reviewed by Binkley, 1996; Rhoades, 1997; Binkley and Giardina, 1998). These include: the deposition of above-ground litter fall (Zinke, 1962; Lodhi, 1977; Leite and Valle, 1990); the release and decomposition of below-ground litter and root exudates (Furley, 1975; Singh and Singh, 1993); and, stemflow and throughfall (Gersper and Holowaychuk, 1971; Andersson, 1991; Ko and Reich, 1993). Tree roots and associated mycorrhizae explore large volumes of soil for nutrients used for plant growth and function. A portion of these nutrients are returned to the soil as above- and below-ground litter which may accumulate in surface soils under the tree canopy. However, as noted by Binkley (1996), few studies have distinguished between the influence that trees have on soil, and *a priori* differences in soil that influence patterns of tree establishment, survival, and growth.

In the present study, we established that concentrations of plant-available P and N, and total P, N and C were higher in soils near stems than in soils from beyond the canopy dripline. These pre-disturbance patterns in soil nutrients have two interpretations. First, the trees redistributed nutrients in soil. Alternatively, a priori differences in soil nutrients modified patterns of tree establishment. Distinguishing between the two interpretations is not possible because the forest was naturally occurring, and no pre-establishment soil data are available. However, biologically active pools of soil nutrients differed significantly between stem and dripline soils, and concentrations of biologically active P in soil declined substantially within 1 m of the stem (Figure 2). Further, concentrations of non-plant-available P (non-biologically active P) did not differ significantly between stem and dripline soils (Tables 4 and 5). For these reasons, we suggest that stem-related patterns were due at least in part, to modification of the soil by the trees. We note that establishing the presence of pre-disturbance soil nutrient patterns was necessary for testing the main hypothesis of this pa-

Table 9. Initial extractable ammonium and nitrate, and net N mineralization and nitrification rates in 0.02–0.10 m depth soils for *C. eriostachys*. A paired *t*-test was used to make comparisons between stem and dripline soils for each nitrogen measure. Comparisons were not made between treatment periods. (n=10)

Treatment	Location	*Caesalpinia eriostachys* 0.02–0.10 m soil depth			
		Initial extractable (μg N g^{-1} soil)		Transformation rates (μg N g^{-1} soil mo^{-1})	
		Ammonium	Nitrate	Net N mineralization	Net nitrification
Pre-burn					
	stem	11.1 a	30.3 a	89.3 a	99.5 a
		(3.3)	(8.4)	(11.8)	(13.8)
	dripline	6.7 a	7.4 b	46.6 b	52.4 b
		(0.9)	(2.9)	(5.4)	(5.5)
Post-burn					
	stem	123.9 a	1.9 a	60.1 a	62.3 a
		(26.1)	(0.7)	(17.6)	(26.4)
	dripline	59.2 a	3.1 a	72.0 a	76.5 a
		(17.4)	(1.0)	(9.8)	(14.2)
Post-growing season 1	stem	44.9 a	39.5 a	33.6 a	77.8 a
		(22.4)	(13.4)	(8.6)	(17.6)
	dripline	6.1 a	6.9 b	18.6 a	24.7 b
		(1.5)	(2.0)	(3.8)	(4.4)

Note: Data are means with standard errors in parentheses. Means followed by different letters denote a significant difference at P<0.05. Pair-wise comparisons are only for columns within treatment periods.

Table 10. Total soil carbon and nitrogen in 0–0.02 m depth soils. Two-way ANOVA split plot analyses were used to make comparisons between species and between stem and dripline soils for each element. Comparisons were not made between treatment periods. (n = 6)

Treatment	Location	Carbon (%)		Nitrogen (%)	
		C. eriostachys	*F. pallida*	*C. eriostachys*	*F. pallida*
Pre-burn					
	stem	10.0 a	9.3 a	0.79 a	0.96 a
		(1.1)	(1.4)	(0.08)	(0.13)
	dripline	4.6 b	5.6 b	0.46 b	0.62 b
		(0.6)	(0.5)	(0.06)	(0.06)
Post-burn					
	stem	3.9 a	5.2 a	0.42 a	0.68 b
		(1.0)	(0.9)	(0.09)	(0.08)
	dripline	3.4 a	4.2 a	0.38 a	0.52 b
		(0.6)	(0.7)	(0.05)	(0.09)
Post-growing season 1	stem	4.4 a	4.9 a	0.45 a	0.61 b
		(0.8)	(0.3)	(0.07)	(0.07)
	dripline	2.6 b	4.3 b	0.29 c	0.52 d
		(0.2)	(0.4)	(0.03)	(0.07)

Note: Values are means with standard error in parentheses.
Means followed by different letters denote a significant difference at $P < 0.05$.
Pair-wise comparisons are only for rows and columns within treatment periods.

Table 11. Total soil carbon and nitrogen in 0–0.02 m depth soils. Two-way ANOVA split plot analyses were used to make comparisons between species and between stem and dripline soils for each element. (n = 6)

Treatment	Location	Carbon (g C m^{-2} soil)		Nitrogen (g N m^{-2} soil)	
		C. eriostachys	*F. pallida*	*C. eriostachys*	*F. pallida*
Pre-burn					
	stem	1205 a	1412 a	95 a	146 b
		(132)	(212)	(10)	(20)
	dripline	635 b	922 b	63 c	104 d
		(84)	(83)	(8)	(10)

Note: Values are means with standard error in parentheses.
Means followed by different letters denote a significant difference at $P < 0.05$.
Pair-wise comparisons are only for rows and columns within treatment periods.

Table 12. Tree basal diameter, height, canopy area, and % slope for both species. A Student's t-test was used to make comparisons between species. (n = 10)

Species	Basal diameter (m)	Height (m)	Canopy area (m^2)	Slope (%)
Caesalpinia eriostachys	0.48 a	9.4 a	41.0 a	27.2 a
	(0.03)	(0.4)	(5.1)	(4.6)
Forchhammeria pallida	0.20 b	5.8 b	13.6 b	27.1 a
	(0.01)	(0.4)	(3.0)	(4.7)

Note: Values are means with standard errors in parentheses.
Means followed by different letters denote a significant difference at $P < 0.05$.

per, that stem-related patterns in soil nutrients do not persist following disturbance.

Post-burn stem effects

Soil temperatures were higher and nutrient transformations larger for 0–0.02 m depth soils as compared to 0.02–0.10 m depth soils. It was likely that burning intensity and soil heating varied between stem and dripline locations because of the larger quantities of litter, higher concentrations of soil C, and lower bulk densities observed near tree stems. This view is supported by the observation that slash burning resulted in a significant stem effect for soil pH. The larger increase in pH near stems was likely due to higher soil temperatures and higher consumption rates of initially larger quantities of organic matter in stem soils.

The large post-burn increase in labile Pi for this site was shown to be due primarily to the thermal mineralization of nutrients associated with soil organic matter, and secondarily to ash inputs from consumed above-ground biomass (Giardina et al., 1999). The increase in plant-available P and decrease in non-plant-available P observed here are consistent with this interpretation. The small post-burn increases in the labile Po fraction (Tables 2 and 3) may be related to the release of nucleic acids, phospholipids, phosphate sugars, and other Po compounds from heat lysed microbes and from solubilized soil organic matter-P (Serrasolsas and Khanna, 1995). The increases in the NaOH Pi fraction may represent a heat induced breakdown of soil aggregate structure (Giovannini et al., 1988) which caused new mineral surfaces to be exposed to the NaOH extract solution. The post-burn decrease in the NaOH Po fraction for 0-0.02 m stem soils under both species was likely due to oxidation of organic matter and microbial biomass (Giovannini et al., 1990; Serrasolsas and Khanna, 1995; Giardina et al., 1999). Larger losses of NaOH Po for 0-0.02 m stem than dripline soils (Table 2) is consistent with the interpretation that temperatures were higher in stem soils.

Losses of soil N can occur when soils are heated to temperatures as low as 100 °C (DeBano et al., 1979; Raison, 1979; Kutiel and Shaviv, 1989). The larger N losses from stem than dripline 0–0.02 m depth soils (3.7 and 2.8 mg g^{-1}[stem] versus 0.8 and 1.0 mg g^{-1} [dripline] for *C. eriostachys* and *F. pallida*, respectively; Table 10) were likely due to higher

temperatures in stem soils. When soils are heated above 100 °C there is typically a large increase in extractable NH_4^+. The observed increases in NH_4^+ concentrations at both soil depths and both sample locations were likely due to the thermal decomposition of organic matter (Russel et al., 1974), the release of fixed NH_4^+ from soil minerals (Raison, 1979), and the death and subsequent release of N from microbial biomass (Raison, 1979). Nitrate is lost above 150 °C as volatilized nitric acid (Raison, 1979), explaining the large decrease in extractable NO_3^- in 0–0.02 m depth soils. The decrease in NO_3^- for 0.02–0.10 m depth stem soils indicates that temperatures may have exceeded 150 °C in these soils. Raison (1979) reports that soil sterilization occurs when soils are heated above 127 °C. Therefore, microbial communities in surface soils were almost certainly impacted by the high soil temperatures observed during burning at this site. The post-burn decreases in net N mineralization and nitrification rates in stem soils were likely due to heat induced death of soil microbes (Serrasolsas and Khanna, 1995). As a result of slash burning, significant stem effects were eliminated for KCl extractable NO_3^-, total N, and net N mineralization and nitrification rates.

Losses of soil C can occur at temperatures above 300 °C (Sertsu and Sanchez, 1978; Raison, 1979). The pre-burn stem effect for total C did not persist following burning because there were larger losses of total C in stem versus dripline soils during burning (61.4 and 41.2 mg g^{-1}[stem] versus 12.0 and 13.3 mg g^{-1} [dripline] for *C. eriostachys* and *F. pallida*, respectively; Table 10). Losses of soil C were expected because soil temperatures in the top 0.01 m reached well over 300 °C. The post-burn decrease in stem soil C to dripline concentrations may explain the loss of stem effects for net N mineralization and nitrification rates following fire; changes in soil C would directly effect heterotrophic microbial populations that utilize organic C for energy.

Despite the large impact that slash burning had on soil nutrients, stem effects for measures of plant-available P and total P persisted, suggesting that the nutrient mosaic associated with *C. eriostachys* and *F. pallida* remained somewhat intact following disturbance. These findings only partially support our first hypothesis that slash burning would eliminate most of the stem-related patterns in soil nutrients.

Post-growing season 1 stem effects

After the first growing season, during which the research site received over 1000 mm of precipitation, labile Pi, labile Po, and plant-available P decreased from high post-burn concentrations (Tables 2 through 5). With the onset of rains and throughout a growing season, large pulses of post-burn plant-available nutrients in soil are typically reduced by plant and microbial uptake of available nutrients, increased microbial activity, leaching, and geochemical equilibration processes (DeBano and Klopatek, 1988).

The post-growing season 1 increases in NaOH Pi could be due to increased geochemical fixation by soil minerals of a large labile Pi pool, particularly in light of the increase in soil pH. In contrast to a previous suggestion that microbial biomass increases dramatically over pre-burn levels following slash burning and the onset of the rainy season (Nye and Greenland, 1960), we found only small changes in the NaOH Po fraction, which includes microbial P. Our findings suggest little recovery of microbial biomass for *F. pallida*, and less than full recovery for *C. eriostachys* in 0–0.02 m and 0.02–0.10 m depth soils. The continued decrease in net N mineralization and nitrification rates for post-growing season 1 soils is consistent with this interpretation. The decrease in plant-available P and the increase in non-plant-available P was most likely due to the geochemical fixation of pyromineralized labile P. The small change in total P (Table 4) suggests that there was little input of P from ash or that any additions of P from above-ground sources were balanced by exports out of soil. At this site, ash contained low quantities of P (<6 kg ha^{-1}; Giardina et al., 1999) suggesting that fluxes into and out of soil were small.

The post-growing season 1 decrease in soil NH_4^+ concentrations were likely due to: plant and microbial uptake and immobilization; nitrification and fixation of NH_4^+ by clays or other charged soil surfaces; and, potential volatilization losses from a warm, high pH soil. Importantly, while the increase in NO_3^- in these soils indicates that nitrification was occurring, net N mineralization and nitrification rates continued to decrease from already depressed post-burn levels. Losses of NO_3^- due to leaching, either into deeper layers or off site, may also account for declines in total mineral N content. Ash from combusted above-ground biomass typically returns small quantities of N to soil following fire (Raison, 1979) and contained <8 kg ha^{-1} at this site (Giardina et al., 1999). Therefore, in-

corporation of ash into soil during cropping probably had limited influence on soil mineral N content.

Although significant stem effects for all measures of soil N or C were eliminated following burning, stem effects returned for net nitrification rates, total N and C in post-growing season 1 soil. There was also a first time appearance of a significant stem effect for net N mineralization rates in 0–0.02 m depth soils. The changes in soil N and C may have been driven by larger below-ground inputs of roots and above-ground debris into stem than dripline soils, which would influence total C and N, and net N mineralization and nitrification rates. Interpreting changes in stem effects for net N mineralization and nitrification rates is somewhat complicated by seasonal variations in microbial biomass and the cycling rates of soil N (Singh et al., 1991).

Our findings suggest that disturbance may homogenize some patterns of soil nutrients only temporarily, while causing other patterns to become more pronounced. We conclude that the immediate effects of slash burning on soil nutrients may not represent longer-term effects. Overall, these findings do not support our second hypothesis, that cropping and pasture establishment would eliminate stem-related patterns in soil that persisted through slash burning.

Post-growing season 2 stem effects

Changes in soil nutrients that occurred between the first and second growing season (measured under *C. eriostachys* only) were small despite the introduction of cattle onto the site and nearly 1 yr of grazing. Labile Pi and Po generally decreased, suggesting that plant uptake, microbial activity, and geochemical equilibration processes continued to shift soil P out of more labile pools. NaOH Pi decreased at the stem, with little change at the dripline, indicating that P was also being shifted out of this fraction, either into other more stable soil P fractions or out of the soil. The concentrations of NaOH Po in soil continued to increase for both depths, indicating either a recovery of microbial biomass to pre-burn levels or increased stabilization of inputs of Po following establishment of pasture dominated by perennial grasses.

The reappearance or persistence of significant stem effects for labile Po and NaOH Po for 0–0.02 m depth soils, and for plant-available P at both depths is striking given the extent to which the site had been disturbed. The mechanisms responsible for the persistence of these tree effects have not been previously explored. The persistence of tree effects for some measures of P may be in part related to the low mobility of P in soil, the neutral to basic soil pH of the post-burn site (low net rates of geochemical fixation by soil minerals), the influence of perennial pasture grasses on P cycling, and the distribution of decomposing post-burn debris. The combined effect of these factors could maintain P in plant-available forms, with higher concentrations in stem soils.

It is likely that some of these patterns persisted beyond the length of this study, which suggests that in cases where disturbance is less severe (e.g., single tree mortality), stem-related patterns of soil P may persist for many years. Because P is an important limiting nutrient in many terrestrial ecosystems (Vitousek and Sanford, 1986; Jaramillo and Sanford, 1995), and may play a role in controlling the cycling of other nutrients and C (McGill and Cole, 1981), these findings support the broader hypothesis that trees contribute to the longer-term heterogeneity of soil nutrients. It has been shown that seedling growth of several species of Mexican dry forest trees had contrasting responses to variation in soil nutrient availability (Rincón and Huante, 1994). Therefore, persistent stem-related patterns in soil may also influence post-disturbance patterns of tree regeneration in these dry forests.

Pre-burn species effects

Results from common garden experiments, those examining the influence of randomly assigned tree species on soil, have been mixed (Binkley, 1996; Binkley and Giardina, 1997,1998). For example, in a monospecific plantation study at a lowland site in Costa Rica, Montagnini and Sancho (1994) found no significant differences for soil pH between six indigenous tree species. In contrast, a central Togo plantation study of mono-specific stands of four multipurpose tree species, two of which were N-fixing, documented significantly different soil pH values between species (Drechsel et al., 1991). In a southwestern Wisconsin plantation study, soil pH values differed significantly among the five tree species examined (Son and Gower, 1992). In our study, the absence of species or stem effects on soil pH may indicate that these soils are sufficiently buffered that soils neutralize the influence of trees on soil pH.

Previous tree interaction studies examining soil P have presented varied results with regard to species effects. In the central Togo study, significant species differences were documented for plant-available P in

soil (Drechsel et al., 1991). In a comparison of pure Douglas-fir and mixed Douglas-fir/red alder stands, studies have shown that red alder can significantly alter the size of soil P fractions (Giardina et al., 1995) and P supply (Zou et al., 1995). In contrast, Son and Gower (1992) and Montagnini and Sancho (1994) found no significant differences for plant-available P among plantation tree species. In a mixed-hemlock forest of Kentucky, plant-available P was similar for the two species examined (Boettcher and Kalisz, 1990), and in a Kenyan savanna study, plant-available P was not significantly different between the two species examined (Belsky et al., 1989).

We assumed that dripline soils were beyond the influence of trees, and that dripline soils for *C. eriostachys* and *F. pallida* would be similar with respect to the physical and chemical properties measured, as was found by Rhoades et al. (1994) in a comparison of male and female *Simarouba amara* canopy dripline samples. However, bulk densities and concentrations of non-plant-available P and total P were significantly higher for dripline soils under *F. pallida* than dripline soils under *C. eriostachys*. In this study, the significant pre-burn species effects for dripline bulk density and soil P have two possible interpretations. First, the two species differed in their effects on soil chemical content and physical properties even at the dripline. Alternatively, and more likely, these two species occupied sites with initially different soil properties. The latter interpretation appears to contradict our previous suggestion that differences between stem and dripline soils were due to the influence of trees on soil. However, we suggest that the stem-related and species-related processes influencing patterns in soil nutrients operate at two different spatial scales. At our site, variations in P content of parent material resulted in heterogeneity in the concentration of soil P, with patches that varied on a scale of ∼5 m. This larger-scale heterogeneity apparently influenced tree recruitment and survivorship: *C. eriostachys* occupied low P sites, while *F. pallida* occupied high P sites. The occurrence of *F. pallida* on sites with higher concentrations of non-plant-available P (which includes parent material P) and total P, may indicate that this species is a better competitor on sites with initially higher concentrations of total P. These findings are consistent with previous studies that have documented gender related niche partitioning in some dioecious species, with female individuals occurring on higher P soils than males (Cox, 1981). Spatial segregation of male and female plants also has been attributed to gradients in moisture, pH, sunlight, and elevation (Bierzychudek and Eckhart, 1988). Once established within these larger-scale patches (species effects), trees then redistribute nutrients on a smaller scale of ∼1 m (stem effects) (Figure 2). This redistribution increases within patch heterogeneity by concentrating nutrients near tree stems.

Notably, while the two species differed significantly in basal diameter, height, canopy area (Table 12), and likely litter quantity and quality (Hendricks, 1990; Martinez-Yrizar, 1984; Cook, 1983), the differences in soil nutrients measured between stem and dripline soils were of a similar size for either species. While it is possible that our selection of nutrient measures and sampling design did not capture true differences between species, it is also possible that differences between species did not exist (e.g., Melillo et al., 1989). We caution that deciphering the specific mechanisms responsible for the observed species- and stem-related patterns in soil nutrients will require insights derived from manipulated field experiments.

Post-burn species effect

The first time appearance of species effects for NaOH Po in 0.02–0.10 m depth soils (Table 3) and total N (Table 10) were due to larger Po and N losses in soils under *C. eriostachys*. These nutrient differences were not related to differences in soil pH, which was similar for both species (Table 1). For other nutrient measures, stem or dripline soil nutrients under either species responded similarly to burning. The persistence of species effects for the organic P fractions, with higher nutrient concentrations under *F. pallida* than *C. eriostachys*, indicates that part of the larger-scale nutrient mosaic for soil P remained intact following slash-and-burn disturbance. The inherent immobility of P in soil may have contributed to the persistence of these species effects.

Post-growing season 1 species effects

Differences between species persisted after the first growing season for total N and non-plant-available P, with higher nutrient concentrations in soils under *F. pallida*. The persistence of a species effect for total N, but not for total P or C, is difficult to explain because soil N is more mobile and sensitive to heating and disturbance than P or C. In contrast to P relatively little N is returned via ash to soil following burning.

Conclusions

As has been shown elsewhere, soil properties at our dry forest site varied predictably with proximity to large-stemmed trees. The processes contributing to the spatial heterogeneity of soil nutrients are varied and operate on different scales, resulting in complex patterns in soil (Stark, 1994). Prior to this study, few studies had examined the persistence of stem- or species-related patterns of soil nutrients following disturbance. Our results indicate that both stem- and species-related nutrient patterns in soil do not disappear after trees are eliminated, but instead persist for at least several years through severe disturbance. This study provides strong evidence to support the view that trees create heterogeneity in soils that future trees will be required to exploit. Variation in the ability of different trees to exploit environmental heterogeneity, and the persistence of the influence of trees on soil, indicates that trees can modify subsequent patterns of forest regeneration. Logically, in cases of less severe disturbance (e.g., wildfire, blow-down, insect mortality), stem- and species-related patterns may persist beyond the two year period of this study. Because persistence may be a function of environmental conditions and other site specific variables, our results may be difficult to extrapolate to other sites until the mechanisms responsible for pre-disturbance nutrient patterns, and the persistence of these patterns following disturbance are examined across a range of forest types.

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