Fire effects on the spatial patterns of soil resources in a Nicaraguan wet tropical forest

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Abstract: Anthropogenic wildfires are becoming increasingly frequent in wet tropical forests. This trend follows that of other anthropogenic disturbances, which are now acute and widespread. Fires pose a potentially serious threat to tropical forests. However, little is known about the impact of unintended forest fires on below-ground resources in these ecosystems. This study investigated the influence of fires on the distribution and variability of soil resources on two sets of 50 × 50-m burned and unburned plots in a Nicaraguan rain forest. Samples were collected at 5-m intervals throughout each plot as well as subsamples at 50-cm intervals. Geostatistical techniques as well as univariate statistics were used to quantify the spatial autocorrelation and variability of selected nutrients (N, P and K), carbon and standing leaf litter. Most variability in this forest was spatially dependent at a scale of 30 m or less. However the average range of autocorrelations varied greatly between properties and sites. Burning altered soil heterogeneity by decreasing the range over which soil properties were autocorrelated. Overall the average patch size (range) for nitrogen was reduced by 7%, phosphorus by 52%, potassium by 60% and carbon by 43%. While phosphorus and leaf litter increased in the burned plots compared to unburned plots, potassium was not different. Nitrogen and carbon did not display a consistent pattern between burning regimes and this may be explained by variation in fire intensity. Leaf litter measurements did not correlate with measured soil nutrients within plots. Observed changes in the burned forest were likely a result of both the intensity of burning and change in vegetative cover between the time of the fires and soil sampling.

Key Words: geostatistics, lowland humid tropics, Nicaragua, nitrogen, nutrient, phosphorus, potassium, rain forest, spatial heterogeneity

INTRODUCTION

Forest fires are becoming increasingly common in the wet tropics, a region where burning has been historically rare (Sanford *et al.* 1985, Uhl 1998). High rates of subsistence slash-and-burn agriculture, the most common source of ignition, combined with the drying effects of logging and natural events such as the El Niño–Southern Oscillation are increasing wildfire frequency (Cochrane 1998, Laurance *et al.* 2001, Román-Cuesta *et al.* 2003). The estimated past rate of forest fire occurrence in wet tropical regions is less than once every few hundred years (Sanford *et al.* 1985). At such a low frequency, fire disturbance probably had negligible long-term impacts on forest structure and function. However, the ecological

impact of fire has increased as fires have become more frequent in these forests.

Spatially heterogeneous distributions of soil resources are found in a range of ecosystem types, including agricultural fields (Wendroth *et al.* 2001), deserts (Schlesinger *et al.* 1996), grasslands (Hall 1971) and forests (Gonzalez & Zak 1994, Gross *et al.* 1995, Hirobe *et al.* 2003, Lechowicz & Bell 1991). All of the studies conclude that at the range of metres and below significant spatial heterogeneity of nutrients exists. Noticeably absent from these studies are examples from the wet tropics. However, there are reasons to expect variability. Richter & Barbar (1991), for example, observed that studies in tropical agriculture have long recognized the presence of soil variation, which often creates difficulties for farmers when soil within a field cannot be treated as a homogeneous resource.

Soil nutrient heterogeneity may be defined as the amount of variation in the spatial distribution of nutrients within an area. The terms patchiness and grain are used to define the pattern and scale of this heterogeneity (Ettema &

Wardle 2002, Robertson & Gross 1994). Patchiness is a measure of the spatial dependence of the nutrient distribution and grain refers to the size of the nutrient patches (Ettema & Wardle 2002, Robertson & Gross 1994). A fine-grained soil resource is one with many small patches while a coarse-grained resource is one with fewer, larger patches. However, whether an area is coarse- or fine-grained must be defined in terms of the size of the plant taking advantage of the resource (Vandermeer 1989).

Plants can influence nutrient availability through leaf litter decomposition, root uptake, and by acting as loci for litter accumulation (Boerner & Koslowsky 1989, Jackson & Caldwell 1993). Jackson & Caldwell (1993), for example, showed that bluebunch wheatgrass (*Pseudoroegneria spicata*) strongly influences spatial distribution of nutrients in a Utah, USA, sagebrush-steppe at the scale of less than a metre. Because tropical soils depend on vegetation for nutrient cycling, changes in plant cover should have profound impacts below ground. A forest extensively damaged by a natural wildfire will experience a change in the short- and medium-term vegetative inputs to the soil as the forest recovers. Nutrient heterogeneity and spatial distribution should be expected to increase or decrease depending on the evenness of damage and the changing above-ground inputs.

While much is known about the availability of nutrients in tropical forests, less is understood about the heterogeneity of soil nutrients and the effects of fire on their spatial distribution. The objective of this study was to determine what impact natural wildfires have on the magnitude and spatial distribution of nutrients within a fire-damaged wet tropical forest. Soil nutrient heterogeneity is important because it potentially influences plant species composition (Carson & Barrett 1988) and patterns of succession (Inouye & Tilman 1988).

STUDY SITE

The study was conducted in a lowland wet tropical forest on the Southern Caribbean coast of Nicaragua near the city of Bluefields (11°53′N, 83°58′W, 15–20 m asl). Mean annual temperature for this area is 27 °C and it receives an average annual precipitation of *c.* 4800 mm. Soils in this forest are ultisols with a thin organic layer (< 3 cm) and a moderately thick A horizon (15–20 cm). The soils are acidic with pH ranging between 3.9–4.7 (Picone 2000). The wet season lasts for 9 mo of the year with a short dry season from February through April.

Characterized by a patchwork of forest and farmland, this region, which lies in the agricultural frontier of Nicaragua, was struck in October of 1988 by a category-four storm (Hurricane Joan). The hurricane is estimated to have severely damaged 500 000 ha of forest (Yih *et al.* 1991). The forest is dominated by tree species (> 60

species in a 0.1-ha plot) characteristic of wet tropical, primary-growth neotropical rain forests (Vandermeer *et al.* 2000).

Fires further damaged parts of the forest in May and June of 1998. Regionally, these fires were patchily distributed and while portions of the forest under investigation were burned, some areas were left unaffected (B. Blair, pers. obs.). Similarly, within the burned areas, fire had a variable affect at the scale of metres. Some patches had large trees that were completely scorched and killed, while in other patches, sometimes only metres away, smaller trees had only limited damage to the base of their trunks. Measurements taken in the area 3 mo before and 8 mo following the fires, found a 44% mortality rate of trees greater than 10 cm girth at breast height (J. Vandermeer unpubl. data).

MATERIALS AND METHODS

Sampling method

In March and April of 1999, two 50 × 50-m plots were established (one burned and one unburned) in each of two sites. One pair was located at a site *c.* 15 km north-west of Bluefields adjacent to the Caño Negro River (Caño Negro plots). The other pair (Kukra plots) was located *c.* 25 km south-west of Bluefields near the Kukra River. Burned plots were damaged by fires that occurred 10 mo before the beginning of sampling. Paired plots were chosen based on their proximity and assumed similarity prior to the wildfire. All plots had slopes of less than 5% and similar overstorey species composition. At the Caño Negro site, the unburned plot was 25 m east of the burned plot, while at the Kukra site the unburned plot was *c.* 500 m west of the burned plot.

Within each of the four 50 × 50-m plots a 5-m sampling grid was established (for 121 sample points). In addition, in each plot five randomly placed 2 × 2-m subplots were created with sampling points at 50-cm intervals (for 25 sample points per subplot, 125 sample points per plot). To investigate nutrient heterogeneity and the effects of fire on nutrient availability in this forest, samples of soil and standing leaf litter were collected.

At each sampling point in the plots and subplots, a 0.25 × 0.25-m square was centred over the designated sampling point. In the 50 × 50-m plots, standing leaf litter was collected from within these squares at each point in the 5-m-interval grid. Other plant parts (i.e. woody debris, fruits and flowers) were discarded. Leaf litter was defined as leaves on the forest floor that were at least 50% intact. Leaves broken or decomposed into smaller pieces were considered organic matter and not collected for leaf litter analysis. Leaf litter was the most common constituent of litter in this forest (B. Blair, pers. obs.).

Woody plant parts, the second most common constituent, have significantly lower nutrient concentration than leaf litter (Aber & Melillo 1991) and were not used for this reason. Fruits and flowers were excluded because they are rare and I felt their inclusion might bias individual samples. In the 50×50-m plots and 2×2-m subplots, a soil core (10 cm depth × 6 cm diameter) was taken from each sampling point (the centre of the square) for nutrient analysis. Thus, 121 leaf litter and 246 soil samples were obtained from each site. Leaf litter was dried at $70\,°C$. Soil samples were air-dried and passed through a 2-mm sieve before analyses.

Nutrient analysis

Total nitrogen and carbon were determined through dry combustion by oxidizing 30-mg subsamples of ground soil in a C-H-N analyser (NC2500, CE Instruments, Milan, Italy). Soil phosphorus was determined on 2.5-g subsamples extracted with 50 ml Olsen's solution (Olsen & Sommers 1982) using automated colorimetry (Quick-chem 8000 FIA+, Lachat Instruments, Milwaukee, WI). Available potassium was determined through 1-g subsamples extracted with 10 ml 1M NH_4Cl (Olsen & Sommers 1982) and flame spectrophotometry (Perkin Elmer 403, Perkin Elmer Corporation, Norwalk, CN).

Statistical and geostatistical analysis

Most variables required log-transformation to meet assumptions of normality. The exception to this was phosphorus which was square-root-transformed. In order to determine if standing leaf litter was related to nutrient availability, Pearson correlation matrices between this variables and measured nutrients (N, P, and K) were created. As a general index of absolute variability the coefficient of variation ($CV = s/\bar{x}$) was calculated within each plot for all properties measured. The CV was used to see if the variability of these characteristics had a consistent relationship between the burned and unburned plots or between the Kukra and Caño Negro sites.

Geostatistical methods were used to analyse spatial variation of the measured variables (Robertson & Gross 1994). Semivariance analysis was used to determine if the measured variables were autocorrelated. Semivariance γ at distance interval h is defined as:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_{i+h})]^2,$$

where $N(h)$ is the number of pairs of points separated by h, $z(x_i)$ represents the value of the property at location x_i, and $z(x_{i+h})$ the value of the property at distance interval h from x_i. Semivariograms, which show the change in semivariance over a range of increasing distance intervals, were created for each variable and a curve fitted using a least-squares procedure. Depending on the best fit, a spherical or a linear model was used (Armstrong 1998). Following semivariogram analysis interpolated contour maps of nutrient availability were generated using block kriging (Robertson & Gross 1994).

Ecologically, a semivariogram shows graphically whether there is a spatial component to observed variability (the degree of patchiness) and the strength of this spatial component (the discreteness of patches) (Robertson & Gross 1994). A semivariogram has four basic elements, the error (C_o), structural (C), and population ($C_o + C$) variances, and the range (A_o). The structural variance is the variability explained by the geostatistical model. To estimate the magnitude of spatial dependence, the proportion of population variance caused by structural variance was calculated for each variable [$C/(C_o + C)$]. Once a semivariogram reaches its limiting value (population variance) there is no longer any correlation between samples. The distance between this point and the origin is termed the range. A large range indicates a coarse grain structure of the measured variable (large patches) whereas a small range indicates a more fine grain structure (small patches). In a linear model, the range is undefined because the measured area is not large enough to define patch size. All geostatistical analysis was performed using GS^+ version 3.11 (Gamma Designs Software, Plainville, MI) computer software.

RESULTS

Variation among plots

The relationships between plots varied for different variables (Table 1). Total nitrogen and carbon at the Caño Negro site were higher in the unburned plot. However, at the Kukra site the opposite trend was observed, both nitrogen and carbon were lower in the unburned plot. Phosphorus availability in the burned plots was higher at both sites, while potassium availability was similar in burned and unburned areas. Standing leaf litter was lower in both burned plots.

Variation within plots

The coefficient of variation (CV) was used as a relative measure of overall variation of the variables in individual plots (Figure 1). In this study, nitrogen and potassium tended to have low CVs in the range of 12–30%. Total carbon, while having similar low-end values, had a higher top-end with a range between 8–52%. Finally,

Table 1. Summary statistics for the burned and unburned plots at each site. Values shown are means $\pm$ SE (N = 121 for leaf litter and leaf area index, and 246 for all other variables).

Soil property	Caño Negro		Kukra	
	Unburned	Burned	Unburned	Burned
Total nitrogen (mg g^{-1})	5.4 ± 0.04	4.2 ± 0.10	5.7 ± 0.10	9.1 ± 0.10
Phosphorus (μg g^{-1})	2.89 ± 0.14	4.53 ± 0.18	3.54 ± 0.21	7.60 ± 0.18
Potassium (cmol kg^{-1})	0.27 ± 0.004	0.28 ± 0.01	0.45 ± 0.01	0.44 ± 0.01
Total carbon (mg g^{-1})	54.6 ± 0.50	42.7 ± 0.70	69.8 ± 2.30	104.8 ± 1.70
Leaf litter (g m^{-1})	19.1 ± 1.22	9.7 ± 0.78	44.2 ± 0.46	39.0 ± 1.99

phosphorus and leaf litter displayed the most variation of all variables examined with CVs between 36–92%. No correlations were found between leaf litter and nutrients.

Spatial variation between sites

Geostatistical analyses revealed that most variables were strongly autocorrelated at short distances and were fitted well with a spherical model (Table 2). Curves of semivariograms fitted with spherical models had an average r^2 value of 0.76. Similarly, the proportion of total variance accounted for by spatially dependent variance $[C/(C + C_o)]$ was high on average (80%).

The average range of autocorrelations varied greatly between sites (Table 2). Within Caño Negro, for example, semivariograms for nitrogen and carbon displayed average ranges of 4.3 m (C) and 4.7 m (N). However, in Kukra these same variables had larger ranges of 22.2 m (C) and 17.7 m (N). Carbon and nitrogen at Kukra thus had ranges 400% or higher than at Caño Negro. Similar

differences in range were found for potassium but here ranges were higher in Caño Negro $[A_o = 9.7$ m (Caño Negro), $A_o = 3.1$ m (Kukra)].

In general, burning reduced the average patch size of soil properties (Table 2, Figures 2, 3 and 4). The mean patch size (range) for carbon in Kukra, for instance, was reduced by 55% (31 m vs. 14 m) when the unburned and burned plots are compared. Similarly, phosphorus was reduced by 50% (7.0 m vs. 3.5 m), potassium by 40% (3.8 m vs. 2.3 m), and nitrogen by 30% (21 m vs. 14 m). A similar pattern was observed in Caño Negro with the exception of nitrogen.

Spatial variation within sites

When comparing variables between burned and unburned plots within an individual site, most model statistics showed no distinct pattern (Table 2). The exception to this was the range over which variables were autocorrelated. In general, variables showed a greater
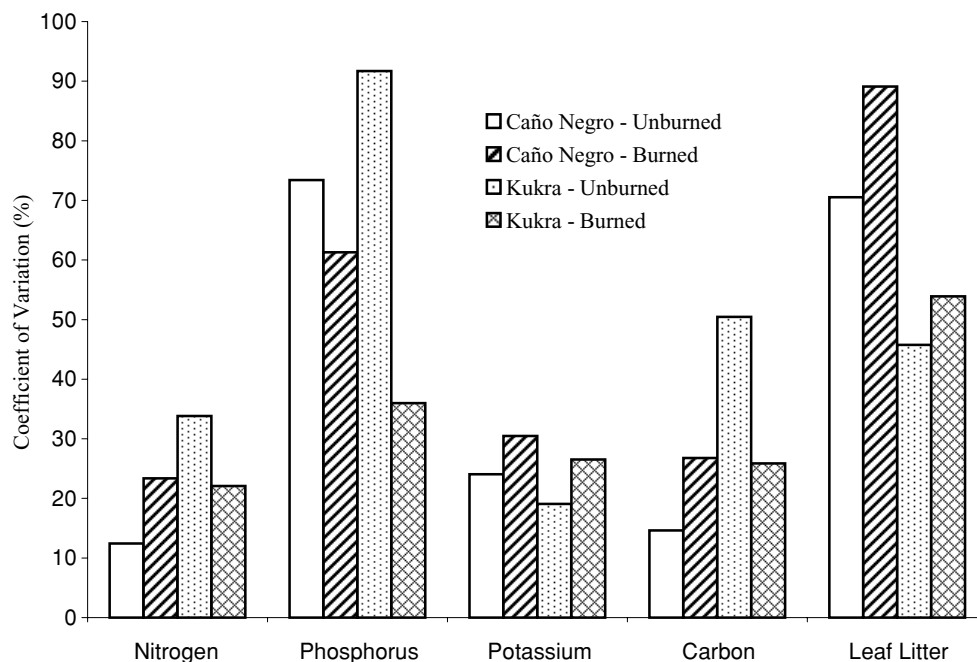

Figure 1. Coefficient of variation of measured variables in each plot of the Caño Negro and Kukra sites.

Table 2. Spatial statistics for all variables in the burned and unburned plots of the Caño Negro and Kukra sites. The best-fit model is presented for each variable (S = spherical, L = Linear). Proportion is defined as the proportion of total variance accounted for by spatially dependent variance $[C/(C+C_o)]$ and is an indicator of the magnitude of spatial dependence of each variable.

Site (damage)	Model	r^2	Error (C_o)	Sill ($C + C_o$)	Range (m)	Proportion (%)
Caño Negro (unburned)						
Total nitrogen	S	0.74	0.006	0.023	4.3	74
Phosphorus	S	0.82	0.142	0.446	11.6	68
Potassium	S	0.77	0.001	0.005	10.8	80
Total carbon	S	0.92	0.001	0.005	5.1	80
Leaf litter	L	0.48	0.546	undefined	> 50	undefined
Caño Negro (burned)						
Total nitrogen	S	0.80	0.024	0.071	5.4	66
Phosphorus	S	0.83	0.176	0.353	5.3	50
Potassium	S	0.80	0.034	0.076	8.6	55
Total carbon	S	0.56	0.002	0.010	3.5	79
Leaf litter	L	0.73	0.293	undefined	> 50	undefined
Kukra (unburned)						
Total nitrogen	S	0.82	0.041	0.177	21.2	77
Phosphorus	S	0.78	0.176	0.770	7.0	77
Potassium	S	0.68	0.008	0.035	3.8	78
Total carbon	S	0.96	0.017	0.137	30.8	88
Leaf litter	L	0.82	0.178	undefined	> 50	undefined
Kukra (burned)						
Total nitrogen	S	0.84	0.002	0.068	14.1	97
Phosphorus	S	0.87	2.48	7.38	3.5	66
Potassium	S	0.42	0.011	0.055	2.3	80
Total carbon	S	0.79	0.0001	0.052	14.0	100
Leaf litter	L	0.90	0.220	undefined	> 50	undefined
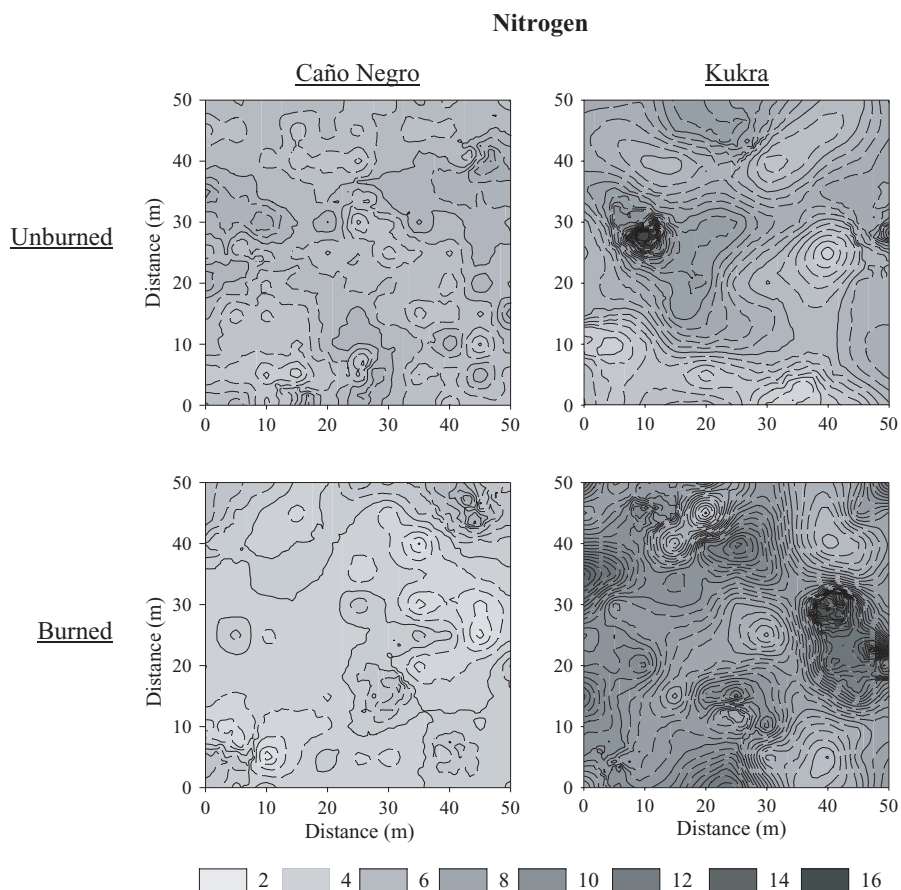
Figure 2. Block kriged (interpolated) contour maps for total nitrogen (mg g^{-1}) in 50 × 50-m unburned and burned forest plots.
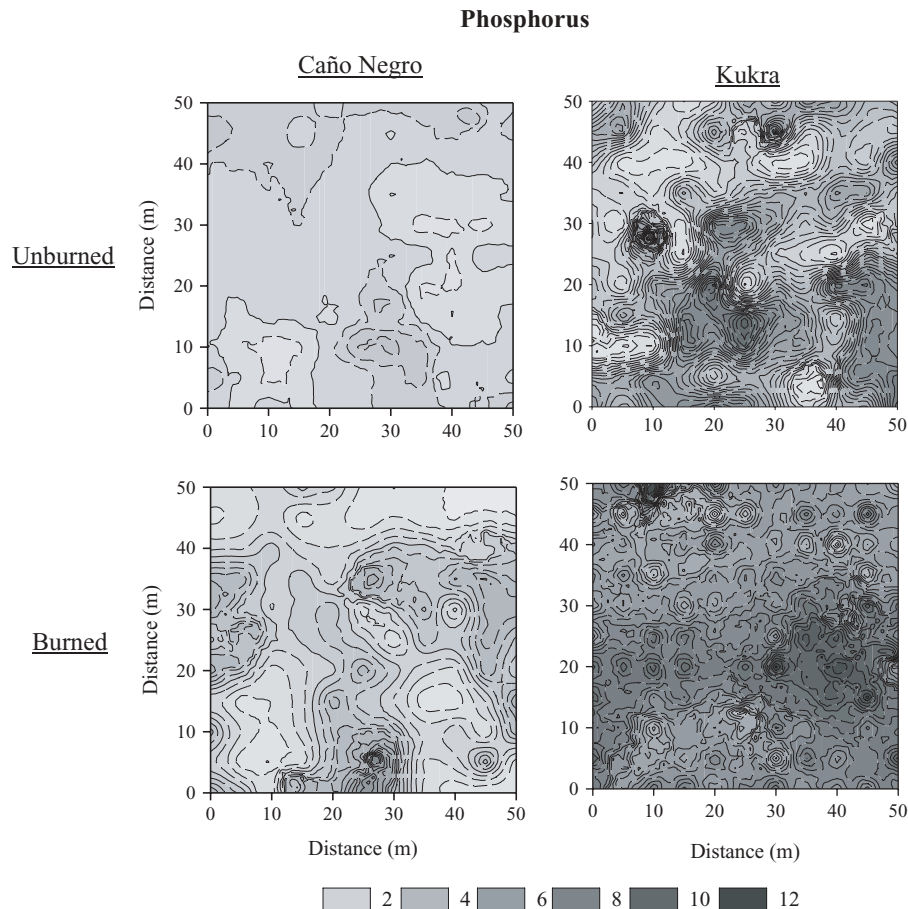
Phosphorus

Figure 3. Block kriged (interpolated) contour maps for available phosphorus ($\mu g\ g^{-1}$) in 50×50-m unburned and burned forest plots.

range in the unburned plots than burned plots when compared within a given site. Physically, this means that average patch size in the burned plots was smaller than patch size in the unburned plots. This trend did not hold true in Caño Negro for nitrogen and leaf litter, or in Kukra for leaf litter.

DISCUSSION

Soil properties

Burning had a great impact on the overstorey of the forest. At the time of measurement, 10 mo after burning, standing leaf litter was reduced by 50% in Caño Negro, but only by 8% in Kukra (Table 1). The relatively small reduction in Kukra of leaf litter at the burned site was likely due to a greater abundance of herbaceous understorey plants and tree saplings in Kukra than in Caño Negro (B. Blair, pers. obs.). Nutrient data suggest that the increased understorey growth in Kukra may be attributed to less-severe burning in this area.

Fire temperature at the soil surface affects whether burning may increase or decrease nutrient availability. In fires where the soil surface stays below $100\ ^{\circ}$C, nutrients held within the plant matter are released in the form of ash to the soil surface and nutrients held in organic matter in the first few centimetres of soil are left unaffected. When soil temperature rises above $100\ ^{\circ}$C, organic matter starts to burn, and above $200\ ^{\circ}$C nutrients can be lost to volatilization (Giovannini *et. al.* 1990). Of the nutrients measured in this study, nitrogen volatizes at the lowest temperatures while phosphorus and potassium are more resistant (Cook 1994, Debano *et al.* 1998, Raison *et al.* 1985).

Evidence from nutrient analysis suggests that the fires in Caño Negro were hotter than those in Kukra. Soil total nitrogen and total carbon were both lower in the burned plot at Caño Negro, but higher in the burned plot at Kukra. This was likely due to greater volatization of nitrogen and carbon in the organic matter incorporated into the upper centimetres of the soil and leaf litter at Caño Negro. Phosphorus levels were higher in both burned plots, suggesting soil P was not volatized during burning and
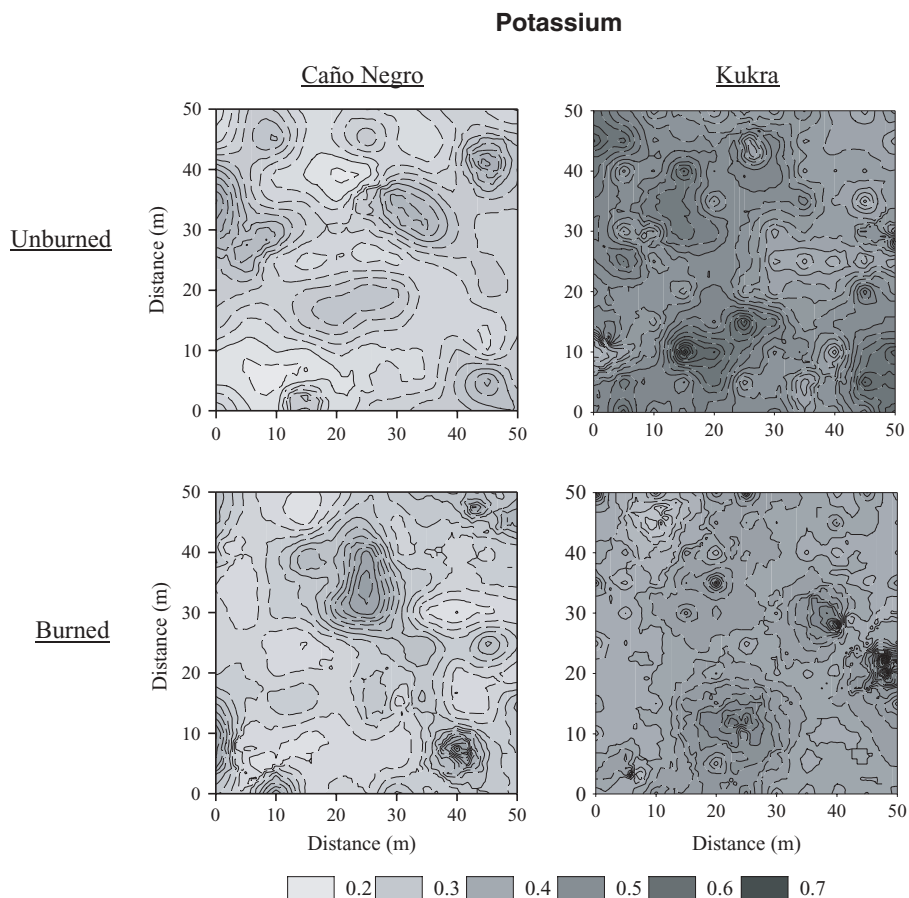
Potassium

Figure 4. Block kriged (interpolated) contour maps for available potassium (cmol kg^{-1}) in 50 × 50-m unburned and burned forest plots.

that a portion of the phosphorus stored in plant material was introduced to the soil in ash deposits. Potassium availability changed little between plots at the two sites, and the high temperature necessary for volatization of this element suggests that it was unlikely to be volatized in large quantities. Increased availability of potassium was not found. However, this was not unexpected because potassium has a high propensity to leaching (Brady 1990, Forgeard & Frenot 1996) and there was a 10-mo delay between burning and initial sampling.

While soil nutrients had a variable response to the fire depending on the nutrient and site, nutrient loss to the system as a whole was likely significant (Caldwell *et al.* 2002, Mackensen *et al.* 1996). In the Amazon it is estimated that 27–33% of P is lost to the atmosphere during agricultural burning (Mackensen *et al.* 1996). Loss of N due to volatization may be even higher (Raison *et al.* 1985). While the forest in the current study was not completely destroyed, previous mortality measurements of burned areas in this forest suggest significant system-wide nutrient loss. Fire-damaged forests in the wet tropics have a reduced capacity to recycle nutrients and are more susceptible to future fires than undamaged stands

(Cochrane 1998). Current conditions of burned forests are therefore not a good predictor of successful forest regeneration.

Variability

The magnitude of the coefficient of variation for soil nutrients and standing leaf litter differed depending on the property being measured and fire history (Figure 1). Overall, burning in this forest increased the variability of standing leaf litter, but no trend was detected for soil variables. Most variability was spatially dependent at a scale of 30 m or less and was represented well by a spherical model (Table 2). However, attributes varied greatly between sites. For example, in Caño Negro carbon and nitrogen both had ranges below 5 m, in stark contrast to carbon and nitrogen in Kukra whose ranges were between 10 and 31 m. Similarly, potassium in Caño Negro had an average range of 10 m but only 3 m at Kukra. These data suggest that generalizations about individual nutrient spatial distributions in tropical forests may not be possible except at a very broad scale.

While burning tended to reduce the average patch size of soil properties (Table 2, Figures 2, 3 and 4) it is unclear what ecological effects this has on the forest ecosystem. Although no ecosystem-level studies examining the competitive effects of nutrient spatial distribution exist, individual- and population-level studies have been conducted (Blair & Perfecto 2004, Wijesinghe & Hutchings 1997). Generally, these studies demonstrate that small-scale spatial variation can have an impact on how plants compete for resources below ground. Additionally they suggest that spatial variation changes competitive dynamics within plant communities by creating an environment competitively advantageous for certain species.

Previous geostatistical studies on soil properties have found varying degrees of spatial autocorrelation. Castrignano et al. (2000) found a range as large as 110 m for some soil constituents on a field in Italy. Gonzalez & Zak (1994) found autocorrelations within 50 m for most soil variables in a tropical dry forest in the West Indies. Other studies have found considerably shorter ranges. Palmer (1990) found that for most elements the range of spatial dependence was less than 5 m in a temperate forest in North Carolina.

The spatial distributions of soil properties are strongly influenced by vegetative cover in some habitats (Hirobe et al. 2001, Jackson & Caldwell 1993, Schlesinger et al. 1996). For example, Schlesinger et al. (1996) showed that the size of the spatial range is correlated to the size of canopy cover of vegetation in an area. However, these studies were conducted in areas where plant cover is discontinuous. Shrubs and trees in these environments act as loci for plant debris accumulation which strongly influence soil nutrient availability (Burke 1989, Shlesinger et al. 1990).

In contrast, the current study found no direct link between soil nutrients and standing leaf litter, which is an indirect measure used to infer nutrient input into the soil. Because standing leaf litter is a measure of potential future nutrient inputs, it should be correlated to past litter accumulation. The lack of correlation between nutrients and standing leaf litter is probably due to the continuous and diverse nature of canopy cover and understorey vegetation in tropical forests, which contrasts sharply with the habitats in studies that have found a direct relationship between vegetation and nutrient spatial distribution. Furthermore, the distribution and rate of turnover of fine roots is a potentially important variable not measured in this study (Gill & Jackson 2000, Singh & Singh 1991, Vitousek & Sanford 1986). Although soil nutrients are driven by vegetative inputs in tropical forests (Vitousek & Sanford 1986), quantifying their impact spatially may be difficult.

Soil nutrient levels are fluid properties that are influenced not only by plant deposition, but also by litter decomposition rates and nutrient uptake by plant roots. Litter quality plays an important role in local nutrient availability (Golley 1986) and species differences can affect the rates of litter decomposition and nutrient release (Boettcher & Kalisz 1990, La Caro & Rudd 1985). The forest in the present study sustained severe hurricane damage in 1988 and its current vertical growth rate is rapid (Vandermeer et al. 2001). Thus, standing leaf litter may change significantly over short periods. These complications may further explain why few correlations were found between nutrients and leaf litter.

The present study found that burning altered the nature of soil variability in the forest examined by decreasing the range over which soil variables were autocorrelated. Although, the influence of plants above- and below-ground is likely the major factor affecting soils in the unburned forest, the observed changes in the burned forest were probably a result of both burning and changes in vegetative cover which occurred in the 10 mo between the fires and soil sampling.

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