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Soil Charcoal in Old-Growth Rain Forests from Sea Level to the Continental Divide

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ABSTRACT

Soil charcoal is an indicator of Holocene fires as well as a palaeoecological signature of pre-Colombian land use in Neotropical rain forests. To document rain forest fire history, we examined soil charcoal patterns in continuous old-growth forests along an elevational transect from sea level to the continental divide on the Atlantic slope of Costa Rica. At 10 elevations we sampled 1-ha plots, using 16 cores/ha to collect 1.5-m deep soil samples. We found charcoal in soils at every elevation, with total dry mass ranging from 3.18 g/m^2 at 2000-m elevation to as much as 102.7 g/m^2 at 300 m. Soil charcoal is most abundant at the wettest lowland sites (60–500 m) and less at montane elevations (> 1000 m) where there is less rainfall. Between 30- and 90-cm soil depth, soil charcoal is present consistently and every 1-ha plot has charcoal evidence for multiple fire events. Radiocarbon dates range from 23,240 YBP at 1750-m elevation to 140 YBP at 2600 m. Interestingly, none of the charcoal samples from 2600 m are older than 170 yr, which suggests that forests near the continental divide are relatively young replacement stands that have re-established since the most recent localized volcanic eruption on Volcán Barva. We propose that these old-growth forests have been disturbed infrequently but multiple times as a consequence of anthropogenic and natural fires.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: Costa Rica; disturbance; Holocene; land-use history; Neotropics; palaeoecology; tropical rain forest.

Soil charcoal is an important but often overlooked indicator of fire disturbance in old-growth tropical forests (Sanford & Horn 2000). Charcoal buried in soils provides long-term evidence of fire history. One of the best and most widely appreciated attributes of soil charcoal is that it may provide a large-scale perspective of fire history in areas where lakes and swamps are rare or nonexistent (Horn & Sanford 1992). Examining fire patterns across landscapes is important for understanding long-term disturbance regimes in tropical forest ecosystems. Lowland tropical rain forests burn well under the appropriate conditions (Kaufman & Uhl 1989) and it is possible that tropical forests on any given site have burned infrequently, but several times as a consequence of anthropogenic and natural fires. Abundant evidence for long-term fire histories in the lowland tropics comes from soil charcoal in soil cores, and in sediments from lakes and swamps in the Neotropics (Horn & Sanford 1992, Sanford & Horn 2000, Horn & Kennedy 2001) and Southeast Asia (Goldammer & Siebert 1990). In contrast, Bush *et al.* (2004) recovered almost no sediment charcoal in a region in northwestern Amazonia.

Throughout the tropics, fires have corresponded with periods of high climatic variability, and prehistoric human activity (Haberle & Ledru 2001). Such recent large-scale forest fires in Borneo and Southeast Asia in 1982–1983 and South America in 1997–1998 were human induced and coincided with intense short-term droughts caused by the El Niño Southern Oscillation (ENSO) events (Goldammer & Siebert 1990). As a result, remnant soil charcoal from forest fires is used as an indicator of: (1) past climatic events in the late Pleistocene and Holocene; and (2) prehistoric land use particularly agricultural practices (Bush & Colinvaux 1994, Horn & Kennedy 2001). In tropical moist forests, soil charcoal is usually found in the uppermost 100 cm, and this remnant charcoal may be used to assess the patterns and frequency of ancient fires.

Soil and sediment charcoal from the last 9000 yr have been collected at many sites throughout the Amazon basin (Sanford *et al.* 1985, Saldarraiga & West 1986, Bassini & Becker 1990, Fearnside 1990, Horn & Sanford 1992, Pessenda *et al.* 1996, Turq *et al.* 1998, Sanford & Horn 2000). In Peru and Bolivia (Lake Titicaca) charcoal dates back to 27,500 YBP (Paduano *et al.* 2003). In northeastern Australia, soil charcoal has been dated between 27,000 and 3500 YBP (Hopkins *et al.* 1993), in South Africa between 40,000 and 320 YBP (Cowling *et al.* 1999), and in Southeast Asia (Borneo) between 17,500 and 350 YBP (Goldammer & Siebert 1990). In conjunction with charcoal, pollen from lake and swamp sediments in Southeast Asia reflect anthropogenic disturbances that date back to 10,000–4000 YBP (Flenley 1998).

Late Pleistocene and Holocene charcoal and pollen records in Central America come from Honduras, Nicaragua, Guatemala, Costa Rica, and Panama (Horn 2007). Human populations in the rain forests of Panama have been present for at least 11,000 yr. Sediments from Lake La Yeguada (Panama) provide pollen, charcoal, phytolith, and diatom evidence for reconstruction of late Pleistocene and Holocene climates. The record spans from 20,000 YBP to the present and shows that conditions during the last full glacial period were cooler and at some times dryer than the present. These forests were disturbed extensively by agricultural activities for at least 4000 yr (Piperno *et al.* 1991a, b; Bush and Colinvaux 1994). Exceptionally high accumulation of carbon, phosphorus, and other nutrients as well as charcoal in Terra Preta Anthrosols in contrast with soils in close proximity soils indicates the impact of the pre-Columbian agriculture and land use in Amazonia (Glaser *et al.* 2001). Taken together, previous studies suggest that fires in tropics have been

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caused by human and climatic influences for at least the last 40,000 yr.

Landscape patterns along an elevational transect and age of soil charcoal from rain forest fires are the focus of this research. Previous studies on evidence for rain forest fires in the moist tropics have focused mainly on lowland systems due to the effects of deforestation. Most areas with long elevational transects have also become a patchwork of agriculture, successional and old-growth forests. We propose that investigating the fire history of upland and lowland old-growth rain forests on one slope is important because it links fire disturbance across a series of life zones. Here we describe soil charcoal fragments collected from soils along a 35-km-long transect on the Atlantic slope of Costa Rica established through old-growth rain forests from 60 m at La Selva Biological Station (LSBS) to 2906 m at the continental divide (Volcán Barva).

The main objective of this research is to use soil charcoal in the reconstruction of past land use and fire history to obtain a better understanding of the disturbance and the resiliency of present-day tropical forests. Two hypotheses frame the research developed in this paper. The first is that soil charcoal indicates landscape distribution patterns and age of ancient fires related to human activities, climatic conditions, and volcanic eruptions along this transect. The corresponding soil charcoal ages indicate periods of increased fire probability in this landscape during the Holocene and late Pleistocene periods. The second is that radiocarbon-dated charcoal samples from several soil depths at a specific location provide evidence for multiple fires and a coarse estimate of fire frequency. Taken together, the data describe spatial and temporal fire disturbance patterns at the landscape level.

METHODS

RESEARCH SITE DESCRIPTORS.—Primary rain forest at LSBS in Costa Rica (Fig. 1) was originally described as pristine (Hartshorn 1983), although soil charcoal fragments and pollen signatures in sediments indicate that these forests include areas that were burned (Horn & Sanford 1992) and cultivated by prehistoric inhabitants (Kennedy & Horn 1997, Horn & Kennedy 2001). There is evidence of fires and human impact at high elevation páramo in south central Costa Rica (Horn & Sanford 1992, League & Horn 2000), but there are no data from higher elevations along the LSBS–Volcán Barva transect. Soil charcoal is well studied at the transect base (LSBS) and prior to our research, the oldest evidence for fire (10,650 ± 50 YBP) was recovered there from the intact lowland forest (J. Morris, pers comm.; Table 1). Additional recent work at LSBS suggests that several soil charcoal samples have similar radiocarbon dates (Table 1).

Soil charcoal was measured from soil samples extracted from previously demarcated 1-ha plots in Braulio Carrillo National Park along the LSBS–Volcán Barva transect (Fig. 2; Grieve *et al.* 1990, Lieberman *et al.* 1996). The transect extends 35 km from LSBS to the summit of Volcán Barva (10°00′–10°25′ N and 83°50′–84°10′ W). There are historic references to two eruptions of Volcán Barva during the colonial period—one in 1772 and another in 1867 (Alvarado-Induni 2000). However, Alvarado-Induni (2000) noted that observations made by naturalists who visited the summit area *ca* 22 and 80 yr after the supposed eruptions seem inconsistent with recent volcanic activity. The available historic data do not provide a clear consensus about the latest volcanic activity at Volcán Barva. Alvarado-Induni (2000) mapped several prehistoric lava flows emanating from a series of eruptive foci in the summit area but did not provide dates for different flows.

At LSBS, annual rainfall averages 4015 ± 716 mm and the rainfall increases up to 5000 mm at mid-elevations and decreases toward the extinct volcano summit (Hartshorn & Peralta 1988). Mean monthly temperature is 25.8°C with a 6°C decrease in temperature for every gain in 1000 m (Lieberman *et al.* 1996). The orographic effect of the mountains on the Atlantic slope of this region causes the moisture-laden northeastern trade winds to shape the precipitation patterns (Sanford *et al.* 1994). Two precipitation-based seasons are apparent—a rainy season between mid-April and December and a drier season between January and mid-April but with no month receiving less than 100 mm (Sanford *et al.* 1994). Along the transect, low elevation rain forests do not experience moisture deficit (Sanford *et al.* 1994) whereas the montane forests often do (Marrs *et al.* 1988). There is a gradient of continuous old-growth forest life zones from about ∼ 60 m to upper montane at about ∼ 2900 m (Fig. 2; Holdridge *et al.* 1971, Lieberman *et al.* 1996). Plant species diversity varies along the transect as well with the highest tree diversity at 300 m with 149 species/ha^2 and lowest at 2600 m with 29 species/ha^2.

Soil substrates on the transect are derived from volcanic parent materials with different ages. Soils at the lowest elevation (LSBS) of the transect are Andic Humitropepts on weathered alluvial terraces of the Sarapiquí and Puerto Viejo Rivers (Sollins *et al.* 1994). Highly weathered Andisols occur along most of the Volcán Barva transect (Hartshorn & Peralta 1988). At the uppermost end of the transect (2600 m) we encountered considerable cinder deposits.

SAMPLE DESIGN.—Eleven 1-ha permanent plots were established previously at approximately every 250-m elevation by Operation Releigh (Hartshorn & Peralta 1988) and expanded by Lieberman *et al.* (1996). These plots are located at elevations of 60 (two sites), 300, 500, 750, 1000, 1250, 1750, 2000, 2300, and 2600 m (Fig. 2). All 11 plots along the transect have comparable aspects on relatively level terrain (Lieberman *et al.* 1996). For this study, we divided each 1-ha plot into 25 × 25 m subplots and one core was taken per subplot resulting in a total of 16 subplot cores at each elevation.

Because of the difficulties associated with taking deep compact soil samples by hand in alluvial and allophanic soils, two soil corers were used. A 4-cm radius root corer (Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands) was used for the first 100 cm and a hammer corer (AMS, Slide Hammer, WI, U.S.A.), with a radius of 2.4 cm, was inserted into the same sample hole to collect deep samples from 100 cm to 150 cm. Soil increments were collected in 10-cm sections, producing a total of 15 subsamples from each core. Sampling in each 1-ha plot resulted in 240 10 cm sections (*n*) with a grand total of 2640 (*N*) across the entire transect.

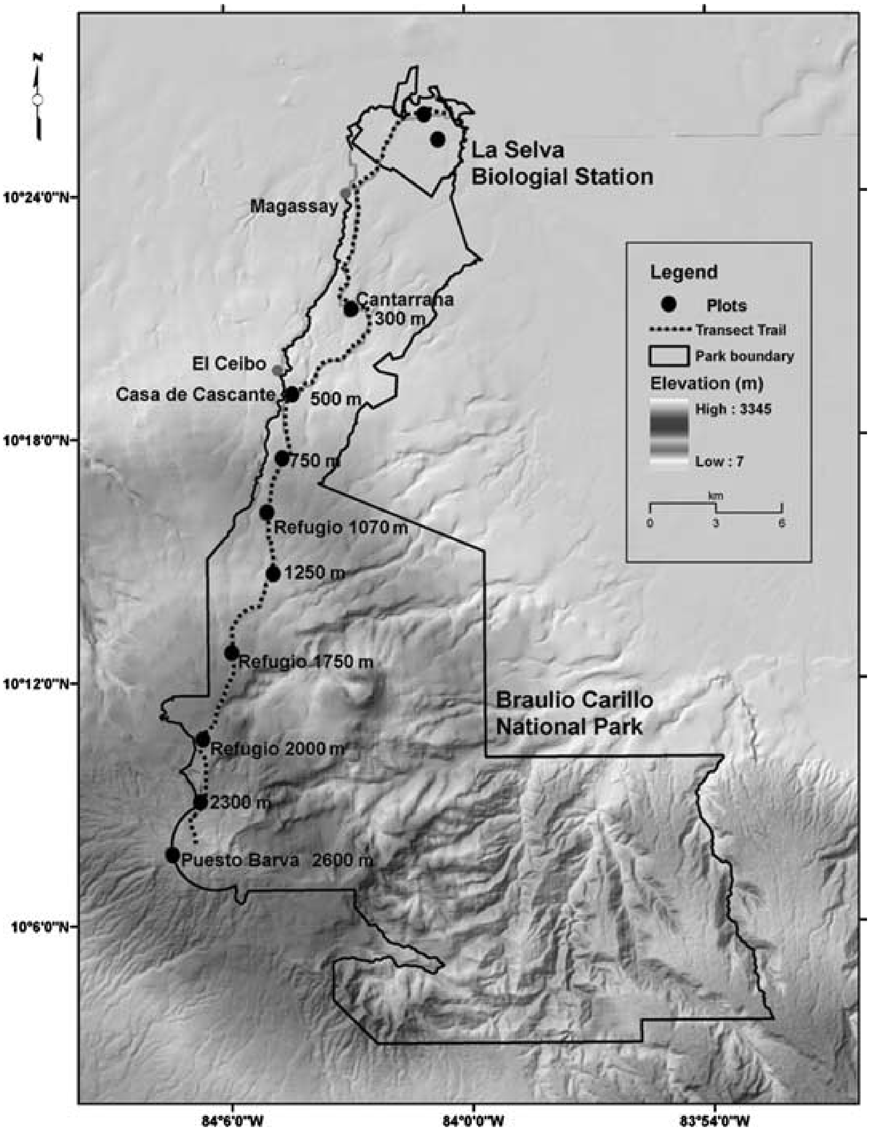

FIGURE 1. General location of the La Selva Biological Station–Volcán Barva transect on the Caribbean slope just over the continental divide from San Jose Costa Rica (Map source: OTS–La Selva Biological Station GIS Laboratory).

Soil samples were sieved (2-mm mesh) and the remaining soil was soaked and rinsed with a dispersant (sodium hexametaphosphate). Subsequently, coarse soil charcoal was carefully hand-sorted from the remaining soil and air-dried. All macroscopic samples were checked for black, angular, and opaque fragments under a dissection microscope to confirm that each of the fragments was produced by fire (Whitlock & Larsen 2001). Multiple charcoal fragments from each 10-cm soil core were weighed together whereas radiocarbon dates were obtained only for individual charcoal fragments from that single core sample. In addition, soil charcoal fragments from across the 1-ha sampling area were weighed to quantify the total charcoal mass of each elevational plot and analyzed for spatial distribution and abundance patterns. Accelerator mass spectrometry (AMS) radiocarbon dates were obtained from Beta Analytic, Inc. (Miami, FL, U.S.A.) for individual charcoal fragments from select subsets of soil samples. One subset (common depth selection) was from 30 cm to 40 cm from six of the 1-ha plots at 300, 500, 750, 1000, 1250, and 2600 m. For the second subset (single-site selection), we used samples at multiple soil depths from 1000-m elevation. At this site, charcoal fragments occurred at multiple depths unlike other plots at higher elevations. Finally, charcoal was dated for 110–120 cm soil depth (1750-m elevation) and for 30–40 cm and 50–60 cm at 2600 m. The last two samples were selected from 2600 m due to the presence of the multiple, unique volcanic cinder layers. Almost every core at 2600 m had such a layer at 10–50 cm overlying a buried soil layer below 50 cm. Charcoal samples from the 60-m sites were not dated due to numerous available dates from nearby sites (Table 1). Overall, the charcoal selected for dating included

TABLE 1. *Depth and age of soil charcoal from previous studies at La Selva Biological Station, Costa Rica. Conventional radiocarbon ages were calibrated using the CALIB v 5.0.1 program* (*Stuiver* et al. *2005*) *and the INTCAL04 data set* (*Reimer* et al. *2004*). *Calibrated ages include minimum and maximum age of all the ranges combined.*

Site	Depth (cm)	Conventional radiocarbon age[f] (YBP)	Calibrated age (YBP)[gh]	Calibrated age (AD/BC)[gh]
La Selva[a]	20–50	2410 ± 220	2959–1899	1010 BC–51AD
La Selva[a]	30–40	2340 ± 80	2703–2153	754–204 BC
La Selva[b]	30–40	2280 ± 40	2352–2157	403–208 BC
La Selva[c]	40–50	2310 ± 40	2452–2157	503–208 BC
La Selva[a]	40–50	1110 ± 70	1238–912	712–1038 AD
La Selva[b]	40–50	190 ± 40	305–35	1645–1915 AD
La Selva[b]	40–50	2220 ± 40	2336–2146	387–197 BC
La Selva[b]	40–50	2590 ± 40	2778–2503	829–554 BC
La Selva[b]	40–50	3020 ± 40	3344–3079	1395–1130 BC
La Selva[b]	50–60	770 ± 40	764–661	1186–1289 AD
La Selva[b]	50–60	2300 ± 40	2361–2156	412–207 BC
La Selva[b]	50–60	2290 ± 40	2355–2157	406–208 BC
La Selva[b]	50–60	2500 ± 40	2739–2366	790–417 BC
La Selva[b]	50–60	6060 ± 40	7144–6791	5195–4842 BC
La Selva[b]	70–80	3090 ± 40	3388–3212	1439–1263 BC
La Selva[c]	90–100	10,650 ± 50	12,822–12,413	10,873–10,464 BC
La Selva[b]	90–100	2870 ± 40	3142–2871	1193–922 BC
La Selva[d]	104–224	805 ± 35	779–675	1171–1275 AD
La Selva[a]	110–120	2340 ± 80	2703–2153	754–204 BC
La Selva[c]	120–130	10,380 ± 50	12,578–12,054	10,629–10,105 BC
La Selva[b]	170–180	230 ± 40	428–30	1522–1920 AD
La Selva[b]	190–200	3130 ± 40	3443–3262	1494–1313 BC
La Selva[e]	244–250	2540 ± 60	2366–2758	809–417 BC

[a] Data from Horn and Sanford 1992.

[b] C. Malone and R. L. Sanford Jr., unpublished data.

[c] J. Morris and R. L. Sanford Jr., unpublished data.

[d] Kennedy and Horn 1997, charcoal dates in conjunction with pollen (*Cantarrana* Swamp).

[e] Horn and Kennedy 2001, charcoal dates in conjunction with pollen (*Machita* Swamp).

[f] All analyses are performed by Beta Analytic Laboratory, Miami, FL, U.S.A.

[g] Stuiver and Reimer 1993, Stuiver and van der Plicht 1998, Stuiver *et al.* 1998, Talma and Vogel 1993.

[h] Calibrations are 2-sigma ranges (95.4%).

specimens from low, mid and high elevations and from a soil depth range of 30–120 cm.

Radiocarbon measurements (^{14}C) are reported in conventional radiocarbon age (YBP) and in calibrated years (cal YBP and AD/BC). CALIB software v. 5.01.1 (Stuiver & Reimer 1993) and the INTCAL04 data set, which were both developed by the Quaternary Isotope Laboratory at the University of Washington (Seattle, WA, U.S.A.), were used to calibrate the conventional radiocarbon age (Reimer *et al.* 2004).

RESULTS

LANDSCAPE PATTERNS: SPATIAL DISTRIBUTION OF SOIL CHARCOAL.—Charcoal was recovered from soils in several depths and in several subplots for every 1-ha plot on the transect between 60-m and 2600-m elevation. Overall, 8 percent of the soil samples had charcoal (211 of 2640). Locally, based on 240 samples per 1-ha plot, soil charcoal frequency ranged between 22.5 percent at 500-m elevation to 1.6 percent at 2300 m (Fig. 3). Charcoal samples were recovered from all soil depths, but was most frequent at 30–90 cm. At lower elevations between 60 m (two plots) and 750 m, 81.2 percent of subplot cores had soil charcoal at some depth. In contrast, soil charcoal was less frequent between 1000 m and 2000 m where only 28.1 percent of subplots cores had charcoal. At 1000 m and above, soil charcoal became progressively less frequent but with a separate, distinct peak in frequency at 2600 m. At the highest sites (2300 m, 2600 m), 31.2 percent of the subplot cores contained charcoal.

Overall, lower elevations (< 1000 m) had more charcoal than higher elevations; however, soil charcoal was found at every plot

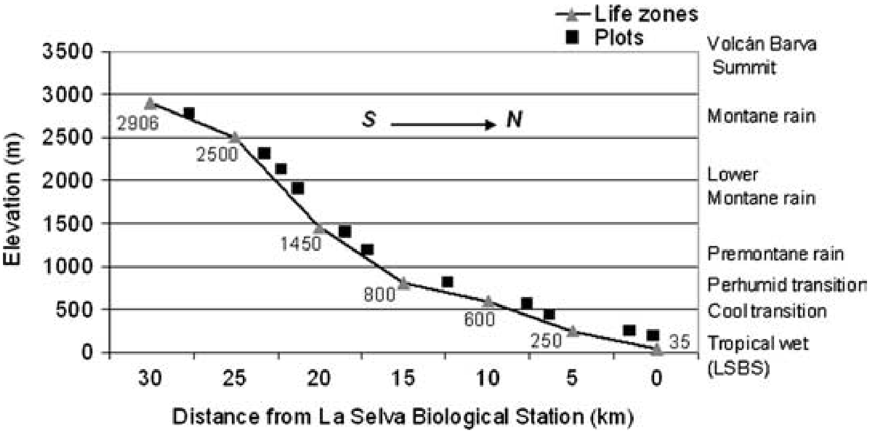

FIGURE 2. Transect cross-section in Braulio Carrillo National Park that includes forest life zones (between triangles), elevation, and the general locations of the eleven 1-ha sample plots (squares) are shown. Distance from the uppermost plot on the continental divide to the lowest 1-ha plot at La Selva Biological Station is shown on the x-axis. Table adapted from Lieberman *et al.* (1996).

ranging from as much as 102.7 g/m^2 at 300 m to as little as 3.18 g/m^2 at 2000 m (Fig. 4). The 1-ha plots at 300 m and 500 m had the largest total charcoal mass at multiple depths (Fig. 5). At higher elevations (>1000 m) the highest charcoal mass (302 g/m^3) occurred at 2600 m at 110–120 cm soil depth. Interestingly, the only site that contained charcoal at every soil depth was at 300 m. Charcoal mass from a single depth (70–80 cm) was largest at 60 m (507 g/m^3; Fig. 5).

TEMPORAL PATTERNS OF CHARCOAL.—For radiocarbon dating, we selected individual charcoal fragments from 11 soil cores (out of a total of 211 samples that had charcoal). The youngest charcoal sample dated to 140 ± 50 YBP at 30–40 cm soil depth at 2600-m elevation, while the oldest fragment dated to 23,240 ± 190 YBP at 110–120 cm soil depth at 1750-m elevation (Table 2). Six samples from the common depth subset (30–40 cm) returned radiocarbon dates of 2190, 2780, 5800, 690, 3570, and 140 YBP, respectively. Four samples from the single-site subset (1000 m) were 690, 220, 350, and 2020 YBP from progressively deeper soils at 30–80 cm (Table 2).

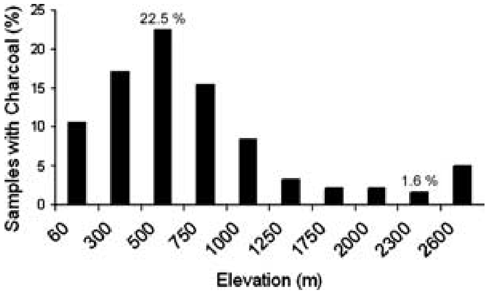

FIGURE 3. Charcoal frequency of occurrence along the transect shown as percent for a single site. Frequency for each elevational site is based on the number of soil cores with soil charcoal fragments/the total soil core samples collected for that elevation (240 samples per elevation).

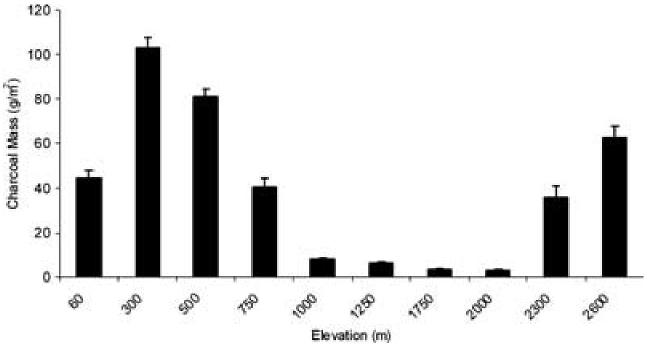

FIGURE 4. Charcoal mass (in g/m^2) of soil charcoal summed for all depths (0–150 cm) and all subplots at 11 plots along the elevational gradient (240 per plot, means ± 2 SE). Site 60-m data are average of two separate sites at this elevation.

DISCUSSION

It is noteworthy and perhaps surprising that fires have occurred from sea level to the continental divide at every 1-ha elevational plot, and at multiple times in these intact tropical rain forests all of which have mean annual precipitation of over 4000 mm and no pronounced dry season. It could be argued that fire is a natural phenomenon given that the sample plots are along the side of a formerly active volcano, but there is no clear evidence of recent activity on Volcán Barva other than possibly the 1772 and the 1867 eruption (Alvarado-Induni 2000). Also the presence of a cinder layer in the soil profile at 2600 m, but not at lower elevations, indicates the likelihood of a localized eruption (such as a small cinder cone)

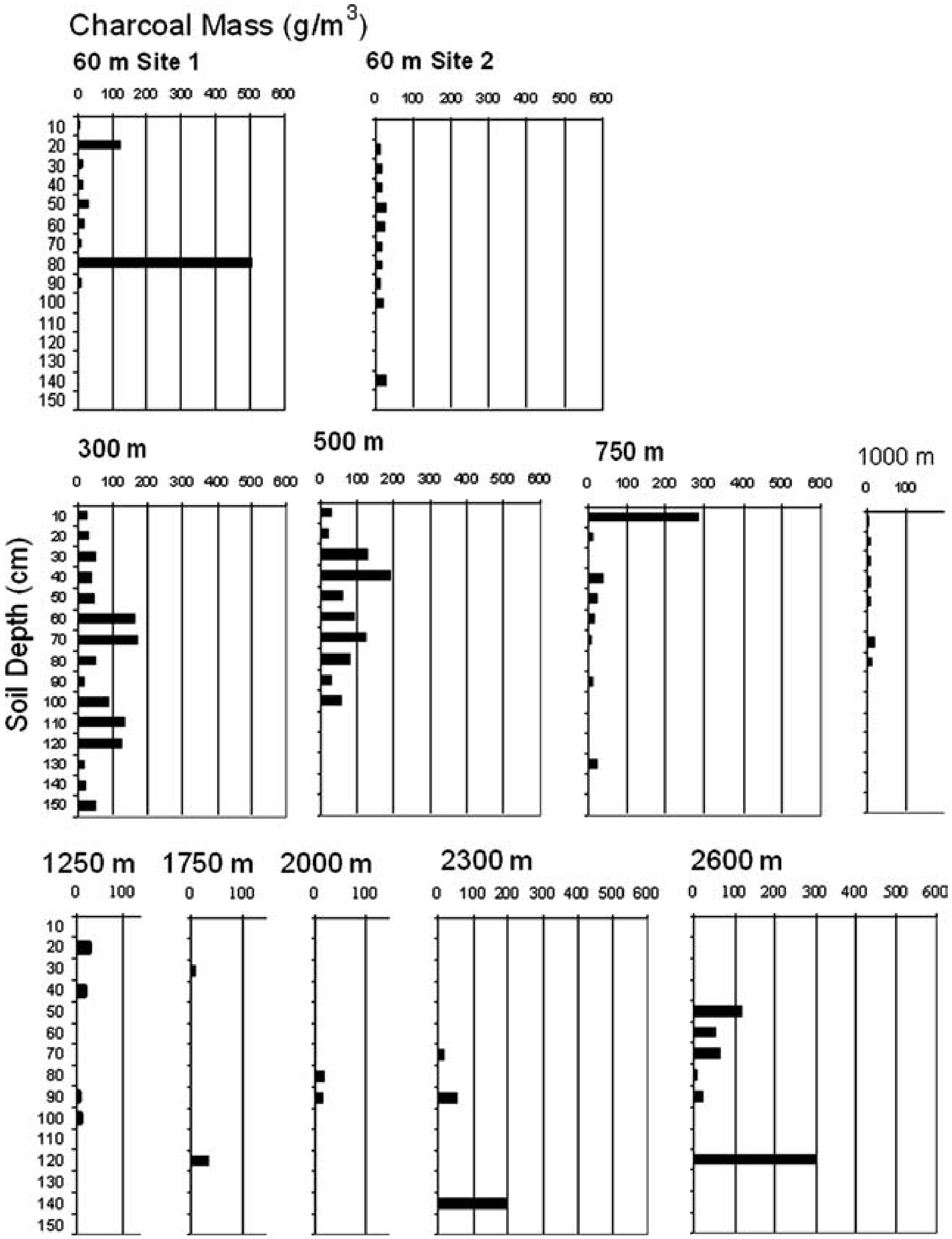

FIGURE 5. Soil charcoal mass at all sites. Shown in g/m^3 for every 10-cm increment from surface soil to 150-cm soil depth. Each bar represents combination of charcoal mass retrieved from 16 subplots in one plot at only one specific depth interval.

rather than a large eruption with extensive downslope effect on forests.

Charcoal was more abundant at lower elevations than at higher elevations. With soil charcoal in 81 percent of cores collected at the lower elevations, there is a clear pattern of frequent ancient fires between 60 m (LSBS) and 750 m. Charcoal fragments are located in adjacent subplots within the 1-ha plots at these elevations, and we interpret this as evidence for agricultural fires that covered no less than a 1-ha area. In contrast, charcoal is not distributed contiguously in subplots at higher elevations (between 1000 and 2300 m) suggesting small-scale or incomplete burns. At higher elevations fires may have been caused by human activity, volcanic activity, or lightning strikes.

The hypothesis that soil charcoal may be used to indicate age and size of the Neotropical ancient fires is supported with various soil charcoal radiocarbon dates. Apart from the two recent ^{14}C dates

TABLE 2. *Elevation soil depth, radiocarbon and calibrated dates of 11 soil carbon samples from the Volcán Barva transect, arranged in three sets: 30–40 cm soil depth at various elevations; multiple soil depths from 1000-m elevation and 2600-m site with cinder layer. Some depths are repeated in the table to emphasize various groups. Conventional radiocarbon ages were calibrated using the CALIB v 5.0.1 program* (*Stuiver* et al. *2005*) *and the INTCAL04 data set (Reimer* et al. *2004). Calibrated ages include minimum and maximum age of all the ranges combined.*

Elevation (m)	Depth (cm)	Conventional radiocarbon age (YBP)[a]	Calibrated age (YBP)[abc]	Calibrated age (BC/AD)[abc]
300	30–40	2190 ± 40	2332–2070	383–121 BC
500	30–40	2780 ± 40	2920–2753	971–804 BC
750	30–40	5800 ± 40	6717–6492	4768–4543 BC
1000	30–40	690 ± 40	692–557	1258–1393 AD
1250	30–40	3570 ± 40	3978–3723	2029–1774 BC
2600	30–40	140 ± 50	283–48	1667–1953 AD
1000	30–40	690 ± 40	692–557	1258–1393 AD
1000	40–50	220 ± 40	425–32	1525–1952 AD
1000	60–70	350 ± 50	499–32	1451–1642 AD
1000	70–80	2020 ± 40	2108–1883	159 BC–67 AD
1750	110–120	23,240 ± 190	23,250	NA
2600	30–40	140 ± 50	283–48	1667–1953 AD
2600	50–60	170 ± 40	295–38	1655–1953 AD

[a] All analyses are performed by Beta Analytic Laboratory, Miami, FL, U.S.A.

[b] Stuiver and Reimer 1993, Talma and Vogel 1993, Stuiver and van der Plicht 1998, Stuiver *et al.* 1998, Reimer *et al.* 2004.

[c] Calibrations are 2-sigma ranges (95.4%).

at 2600-m elevation (140 and 170 YBP), the age of our soil charcoal samples are evidence for many different forest fires ranging from late Pleistocene to late Holocene. The outlier is the charcoal fragment from 1750-m elevation at 110-cm soil depth, which is the oldest by far at 23,240 YBP. Caution should be used to interpret this specific date. AMS dating has potential problems for materials that are older than 20,000 YBP due to the reduced radiocarbon activity of the material.

Soil charcoal with similar radiocarbon ages from multiple 1-ha plots along the slope may indicate the spatial extent or the patchy nature of the fires. Excluding the date > 20,000 YBP, the 10 radiocarbon dates span approximately over 6000 yr (range 140 ± 50 to 5800 ± 40 YBP; Table 2). Some dates from our lower elevational sites correspond well with several intervals of prehistoric burns at *ca* 2000, 3000, and 6000 YBP derived from previously dated charcoal fragments from LSBS (Table 1).

Soil charcoal from the 30–40 cm soil depth at six elevations on our transect and at two sites at LSBS from previous studies (Table 1) returned radiocarbon dates of 2190 (300 m), 2780 (500 m), 5800 (750 m), 690 (1000 m), 3570 (1250 m), 140 (2600 m), 2340, and 2280 (60 m) YBP. There appears to be a consistent age of approximately 2300 YBP at 30–40 cm depth for both LSBS and the transect at only 300 and 500 m. The inconsistency between charcoal ^{14}C ages from different elevations could be a result of a relatively small sample area and the unavoidable patchy sample design of this study.

The ^{14}C analysis of soil charcoal fragments from four depths at 1000 m supports the assertion that charcoal fragments are evidence of multiple fires. Multiple charcoal fragments from the 1000-m plot dated 690, 220, 350, and 2020 YBP at soil depth intervals between 30 and 80 cm, respectively (Table 2). This is robust evidence for multiple fire events at one site. However, the lack of consistency between soil depth and charcoal ^{14}C age suggests that pedoturbation, including tree falls and localized landslides, causes soil charcoal to be relocated within the soil profile.

Several precautions are important to consider when interpreting charcoal radiocarbon dates including the discrepancy between ages of the trees. Charcoal ages reported previously from LSBS may have slightly postdated radiocarbon dates from inbuilt age due to the date when carbon was fixed by the plant, rather than the time of burning (Horn & Sanford 1992). Some of the trees at LSBS are centuries old (*e.g.*, *ca* 530 yr; Fichtler *et al.* 2003). Both 60-m plots are located on alluvial soils that originate from the Sarapiquí River; the potential for fluvial deposition may cause uncertainty in origin of soil charcoal (Sanford & Horn 2000). Spatial parameters (*e.g.*, slope, aspect) of the plots could also introduce background error from variations in depressions, ravines, streambeds, and hilltops regardless of the establishment of plots on similar terrain. Sanford and Horn (2000) suggest that despite the problems of charcoal quantification, location variations, and difficulty in determining ignition sources, soil charcoal analysis is an effective tool for estimating the extent of historical human impact.

The fires at our sites may have been caused by humans (agriculture, land clearance for habitation) or natural causes such as ENSO-related drought, volcanic activity, and lightning strikes. The oldest radiocarbon date (23,240 YBP) can be excluded as a human-induced disturbance because evidence for human settlements did not occur in this region prior to 12,000 YBP (Cooke 1998).

ANTHROPOGENIC SOURCES OF FIRE DISTURBANCE.—Human occupation of the Americas occurred possibly between 12,000 and 11,000 YBP (Cooke 1998) and agriculture started around 10,000 YBP (Smith 1997). To understand anthropogenic influences and land-use history, it is critical to cross-reference soil charcoal with human population fluctuations in the Neotropics.

Paleo-Indian foraging populations in the Neotropics were exploiting and modifying tropical forests in some areas as early as the late Pleistocene/Holocene transition (*ca* 11,200 and 10,000 YBP), with a tropical forest horticulture of native tubers and seed plants developing by *ca* 10,000–8600 YBP (Bonnichsen & Turnmire 1991, Ranere & Cooke 1991, Piperno & Pearsall 1998). Plant domestication and slash and burn cultivation followed, with evidence of the latter apparent at some sites as early as 7000 YBP (Piperno & Pearsall 1998).

Maize pollen can be a valuable cross-reference and good proxy for the ancient agricultural practices mentioned above. Maize pollen, which requires agricultural activities to persist, was retrieved near the lowest sites on the transect in the *Cantarana* and *Machita* swamps at LSBS (Kennedy & Horn 1997, Horn & Kennedy 2001). These pollen samples were cross-referenced with charcoal, which was radiocarbon-dated *ca* 800 and *ca* 2500 YBP (Table 1). Coupled with charcoal radiocarbon dates, the palynological data indicate that fire disturbance was a consequence of agricultural practices.

Pre-Colombian agriculturalists are associated with archeological phases known as La Cabaña at 1150–400 YBP (800–1550 AD) and the *El Bosque* periods at 2250–1650 YBP (300 BC–300 AD) in which human population increased in the Middle Atlantic Watershed (Snarkis 1981, 1984; Kennedy & Horn 1997). A charcoal fragment dated at 690 YBP (1258–1393 AD) at our 1000-m site could correspond to the LSBS pollen and charcoal dated *ca* 800 YBP (1171–1275 AD), and may indicate human activity at 1000 m.

CLIMATIC SOURCES OF FIRE DISTURBANCE.—The charcoal sample from 1750-m elevation dated at 23,240 YBP predates human agriculture and even human habitation in the new world (Smith 1997). This sample may represent a fire that burned during the Last Glacial Maximum (LGM), which is the interval at 27,500–16,800 YBP. Data from Central America and Costa Rica during the LGM indicate colder and drier climate supported by arid vegetation and glacial temperature depressions (Hooghiemstra *et al.* 1992; Orvis & Horn 2000; Horn 2007). In our research, the charcoal fragment that dated approximately 23,000 YBP would then support the natural cause (such as ENSO) hypothesis due to possibly drier climatic conditions. The small ^{14}C data set may have precluded finding other fragments reflecting a drier LGM. Besides, we cannot discount the possibility that the charcoal produced was simply a result of a lightning strike or volcanic activity.

Holocene charcoal may also be an indication of fires that coincide with dry climatic periods such as ENSO in Central and South America; however, ENSO patterns of the tropics during the Holocene are poorly understood. Contradictory climate studies suggest that the Holocene ENSO signal is not uniform for South America (Marchant & Hooghiemstra 2004). In Central America, sedimentary pollen and other indicators suggest wetter and cooler conditions during early to mid-Holocene (about 10,000–5200 YBP) and drier climatic conditions by late Holocene (about 3200 YBP) in the Caribbean region (Hodell *et al.* 1991; Kennedy *et al.* 2006; Horn 2007). These climate patterns and timing do not seem to be consistent all across Central America and South America. Anomalies are considered site-specific variations and are caused by factors, such as volcanic activity, topography, vegetation, soils, and proximity to coasts (Plisner *et al.* 2000). Consequently, a regional variation, such as the intertropical convergence zone, may have caused droughts in this part of Costa Rica.

The greater abundance of charcoal at our lowland sites, relative to higher elevational sites, is intriguing because fire is largely a function of fuel–moisture content. Lowland forests are moisture-saturated whereas montane forests have higher variability in rainfall and are relatively more prone to dry periods (Marrs *et al.* 1988, Sanford *et al.* 1994). Consequently, more fires would be expected at higher elevations when a climate-induced drought occurs. The results of this study suggest the opposite with more abundant soil charcoal as evidence for increased lowland fires. These patterns then suggest there were periods of dry climatic episodes that facilitated human use of lowland forests, while at the higher elevations, dry periods alone were not enough to start forest fires where humans population were not present.

Radiocarbon dating from our research also provides some insight into the controversy concerning the most recent volcanic activity at Volcán Barva. New evidence for a volcanic eruption near the plot at 2600 m comes from the 140 and 170 YBP soil charcoal dates. Interestingly, none of the high-elevation soil charcoal samples are older than 170 yr indicating that the forests near the continental divide may be relatively young, replacement stands that have grown since the last suspected volcanic eruption in 1867 (Alvarado-Induni 2000). We propose that the charcoal from 2600 m is most likely the result of a fire caused by a localized volcanic eruption.

CONCLUSION

Soil charcoal from this study and previous palynological studies from lowlands indicate that intact rain forests along the LSBS–Volcán Barva corridor have been disturbed multiple times by anthropogenic and natural fires during the Holocene. To our knowledge, this study is the first to report soil charcoal in continuous old-growth rain forest from near sea level to montane forest. We hypothesized that different charcoal radiocarbon dates at the same site would indicate the occurrence of multiple fire events whereas observance of multiple similar dates on different sites would indicate extensive area fires. We found that there have been multiple fire events at a single site as well as fires at multiple rain forest sites along this 35-km slope. Further, our results indicate that despite the increased potential for drought at higher elevations, evidence of fire is much more prevalent in the moisture-saturated lowlands due to human activities along the Atlantic slope of Costa Rica. In these rain forests, fires do not normally occur without the influence of drier climatic conditions and are possibly due to severe droughts induced by ENSO or by low soil moisture induced by ancient deforestation (Nepstad *et al.* 1999). It is difficult to separate climatic from human-induced fires, but because there is a feedback loop between drier climate and human activity in the lowland tropics, these influences may combine to create a positive interaction for increased fire frequency (Sanford *et al.* 1985, Haberle & Ledru 2001).

Climate change could be better understood by integrating data from fire disturbance and other palaeoecological studies into larger-scale models. Such integration provides essential insights into the long-term variability of tropical forests and it can also structure a spatial and temporal framework for monitoring future disturbances and ecosystem resiliency in these tropical ecosystems.

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