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Quaternary Research 59 (2003) 79–87

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Paleoecological and archaeological implications of a Late Pleistocene/ Early Holocene record of vegetation and climate from the Pacific coastal plain of Panama

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Received 9 May 2002

Abstract

A phytolith record from Monte Oscuro, a crater lake located 10 m above sea level on the Pacific coastal plain of Panama, shows that during the Late Pleistocene the lake bed was dry and savanna-like vegetation expanded at the expense of tropical deciduous forest, the modern potential vegetation. A significant reduction of precipitation below current levels was almost certainly required to effect the changes observed. Core sediment characteristics indicate that permanent inundation of the Monte Oscuro basin with water occurred at about 10,500 ¹⁴C yr B.P. Pollen and phytolith records show that deciduous tropical forest expanded into the lake's watershed during the early Holocene. Significant burning of the vegetation and increases of weedy plants at ca. 7500 to 7000 ¹⁴C yr B.P. indicate disturbance, which most likely resulted from early human occupation of the seasonal tropical forest near Monte Oscuro and the development of slash-and-burn methods of cultivation.

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Keywords: Pleistocene; Early Holocene; Climate and vegetation; Prehistoric agriculture

Introduction

Although considerable evidence exists for a cooling of at least 6°C and a drier climate over the Neotropical lowlands during the Late Pleistocene (e.g., Guilderson et al., 1994; Stute et al., 1995; Thompson et al., 1995; Colinvaux et al., 1996; Webb et al., 1997; Van der Hammen and Hooghiemstra, 2000), the net effects on plant communities of the competing actions of low temperature, precipitation, and atmospheric concentration of CO₂, together with the magnitude of precipitation reduction, are under considerable discussion (Cowling and Sykes, 1999; Cowling et al., 2001; Colinvaux et al., 2000; Van der Hammen and Hooghiemstra, 2000; Marchant et al., 2001). In Central America south of Guatemala, the few available glacial-age paleovegetational sequences from below 1000 m a.s.l. indicate that the

vegetation was a forest without modern analog (e.g., Bartlett and Barghoorn, 1973; Bush and Colinvaux, 1990; Piperno et al., 1990; Bush et al., 1992). The presence between ca. 16,000 and 10,500 ¹⁴C yr. B.P. of pollen and phytoliths from trees and herbs confined mostly today to higher elevations (e.g., *Magnolia*, *Quercus*, *Ilex*) indicates a significant downward movement of these vegetational elements and a cooling by at least 5°C. These sequences, however, derive from areas where the modern precipitation is between 3000 and 4000 mm. Consequently, they may not adequately inform the problem of environmental change and vegetational response to drier Pleistocene climates in the Pacific watershed lowlands, where the annual precipitation is 2000 mm and less, and forests are more prone to fragmentation.

Detailed reconstructions of Late Pleistocene and early Holocene environments also have considerable importance for understanding the human colonization of the Central American landbridge and subsequent adjustments in human

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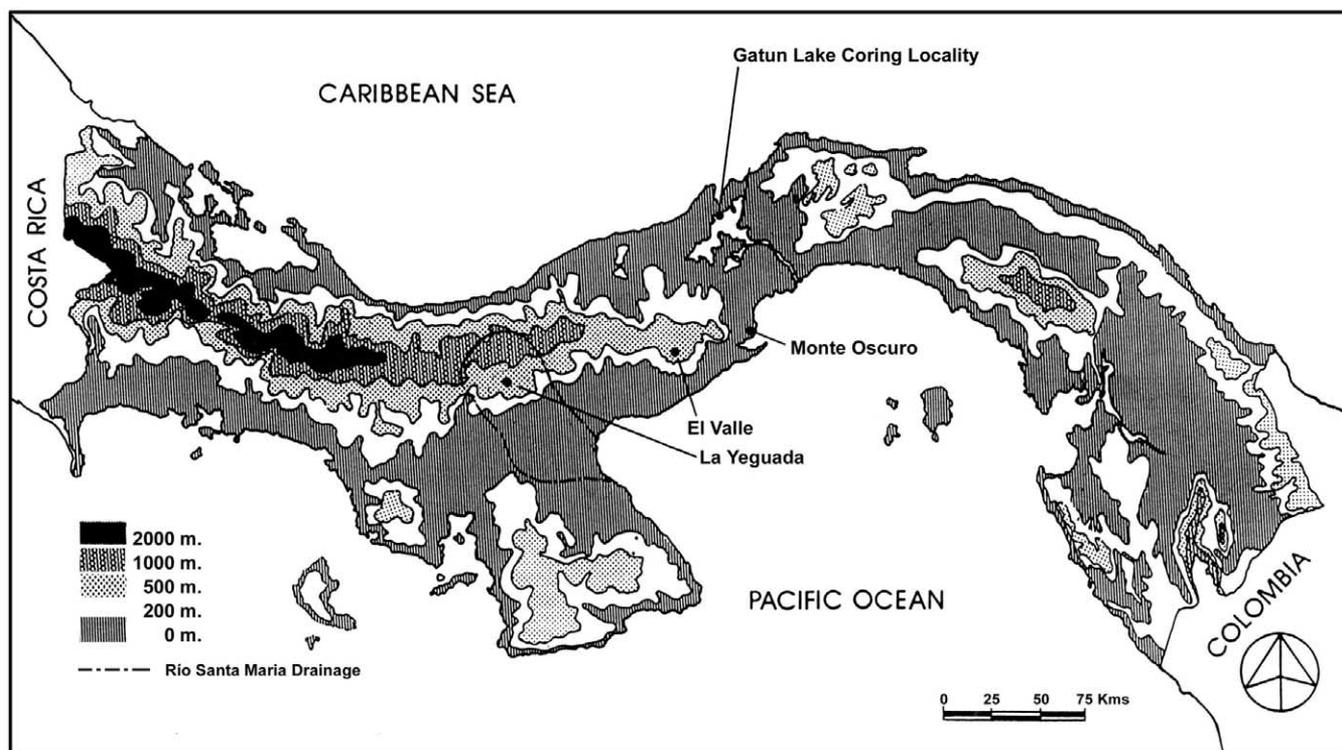


Fig. 1. A topographic map of Panama showing the locations of Monte Oscuro and other sites in Panama that have produced pollen and phytolith records of Late Pleistocene through early Holocene age, together with the Rio Santa Maria archaeological study region mentioned in the text.

subsistence and settlement strategies that led to the origins of agriculture (Piperno and Pearsall, 1998a). Human decision-making concerning the kinds of animal and plant food resources to exploit, and under which modes of production (e.g., hunting and gathering, plant cultivation) to exploit them, is significantly structured by ecological factors relating to the types of vegetational and animal communities present on the landscape through time (Piperno and Pearsall, 1998a; Smith and Winterhalder, 1992). In this paper, we present a Late Pleistocene through early Holocene environmental history based on phytolith and pollen records from sediment cores retrieved from a crater lake, Monte Oscuro, located on the Pacific coastal plain of Panama.

The site and its setting

Monte Oscuro is an extinct volcano located in Central Panama 3 km from the Pacific coast (Fig. 1). The floor of the large (6 × 3 km) crater lies at an elevation of 10 m a.s.l. with the high parts of the caldera rim reaching 340 m a.s.l. During the height of the last advance of glaciers, the site was about 90 km from the sea. The Monte Oscuro region has a strongly seasonal climate in which 90% of the ca. 1800 mm (18-yr average; range 1228–2573 mm) of annual precipitation falls between May and November (Estadística Panama, 1995). The mean annual temperature is 27°C. The potential vegetation is a tropical deciduous forest, most of

which has been cut, although remnants can still be found in areas of the crater that did not hold water and on hills around the site. Monte Oscuro held a permanent lake that occupied a substantial part of the flat-bottomed crater until 1957, when it was drained by local people to create pasture for the cattle industry. Informants who were living in the area when the crater contained water indicate that the water depth was ca. 3–6 m, depending on the time of year. The lake was fed by several inlet streams that drained its small catchment. A small river draining terrain north of the site currently outlets to the sea at the northeastern margin of the crater, and mangrove vegetation from here reaches to within 2.5 km of the coring locale.

Methods

In 1993–1994, we raised two parallel cores 30 m apart, labeled Cores 1 and 2, from near the center of the lake bed using truck-mounted drilling equipment. A steel core barrel 19 cm (7.5 inches) in internal diameter and 2 m in length was forced down by hydraulic pressure to recover sediment, which was then extruded in the field, cut into 1-m lengths, and transported to the laboratory for description and sampling. Subsamples were removed for palynology and phytolith analysis, which were carried out using standard techniques (Faegri and Iverson, 1975; Piperno, 1988). A total of

Table 1
List of ^{14}C dates from Monte Oscuro

^{14}C yr. B.P.	Lab. No.	Depth m. below surface	$^{13}\text{C}/^{12}\text{C}$ ratio
Core 1			
560 \pm 80	Beta-64381	0.26–0.31	–17.7
2290 \pm 60 ^a	Beta-64382	1.90–1.96	–18.2
4750 \pm 170	Beta-68567	2.98–3.0	–25.8
5924 \pm 50 ^b	R 26212/2	3.25–3.35	–26
7500 \pm 70 ^a	Beta-74292	4.75–4.78	–19.4
8380 \pm 60 ^a	Beta-72458	5.70–5.80	–26.2
6190 \pm 60 ^a	Beta-74293	7.00–7.05	–29.2
6890 \pm 60 ^a	Beta-74294	8.02–8.07	–30.4
6040 \pm 60	Beta-74295	8.85–8.90	–26.2
Core 2			
7710 \pm 40	Beta-144636	5.00–5.05	–20.9

^a Indicates an AMS date.

^b Indicates a phytolith AMS date.

26 samples were analyzed for phytoliths and 20 were studied for pollen. In most samples for which pollen and phytolith data are available, sediment from the same stratigraphic depth or contiguous 5-cm levels was analyzed. In pre-Holocene deposits (see below), complementary pollen and phytolith records were not possible due to poor pollen preservation.

Prior to processing, two tablets of exotic *Lycopodium* spores were added to each sample for calculation of pollen concentration. Pollen concentration usually varied between 1600 and 5600 grains/cm³. Pollen and phytoliths were counted to a sum of at least 200 per sample using an Olympus BHS microscope (400–1000x). Phytoliths and pollen were identified by comparison to modern reference collections of over 2000 and 7000 tropical species, respectively, housed in the authors' laboratories. Poaceae phytoliths were identified to subfamily and genus by comparison to over 350 species of Neotropical grasses from all subfamilies of the Poaceae (Piperno and Pearsall, 1998b). Pollen and phytolith diagrams were plotted using TILAGRAPH (Grimm, 1992).

Particulate carbon was counted in the palynological preparations until at least 20 *Lycopodium* spores had been counted. From these counts, estimates of charcoal concentration were obtained. Charcoal classification was restricted to black, completely opaque, angular fragments taken as secure markers of fire by charcoal analysts. When a plant is burned, it leaves behind more than charred organic debris. If the plant holds phytoliths, these are also likely to obtain a black coating indicating charring, and the morphology of the phytolith often remains intact. Knowledge of which plants have been subjected to firing and at what frequency is thus possible through quantification of the percentages of burnt phytoliths in any well-represented taxon.

Core stratigraphy and chronology

Both of the cores terminated in volcanic ash underlying lacustrine sediment and revealed closely comparable stratigraphies upon visual inspection. Core 1 was concentrated on for analysis because it was closest to the deepest part of the lake. Eight ^{14}C dates were obtained on bulk sediment, and one ^{14}C determination was run directly on a phytolith assemblage isolated from the sediment (Table 1). The carbon from plant cells trapped inside of phytoliths provides a suitable substrate for radiocarbon dating, and it is immune to the various modes of post-depositional contamination (Wilding, 1967; Kelly et al., 1991; Mulholland and Prior, 1993). The dates obtained from lacustrine sediments (0–6.7 m) and the phytolith assemblage are internally consistent. There are age reversals at depths below 6.7 m, where AMS determinations on carbon-poor, nonlacustrine silts (7 m) and gravelly subsoils (8 m) appear anomalous. The AMS determination of 5924 \pm 50 ^{14}C yr B.P. on phytoliths derived from watershed vegetation from a depth of 3.25 to 3.35 m is in reasonably good agreement with a date on bulk sediment from 25 cm above. A 7710 \pm 40 ^{14}C yr B.P. determination on bulk sediment from Core 2 is from the same stratigraphic zone and nearly the same depth that returned a date of 7500 \pm 70 ^{14}C yr B.P. in Core 1, further corroborating the chronology for the Core 1 sequence indicated by the dates from 1 to 6 m. A probable cause of the anomalous dates is downward infiltration of relatively young carbon derived from the sediment carbonates (see below) into older strata. That volcanic ashes nearly 1 m below the lacustrine sediments returned an AMS determination similar to the two anomalous dates (Beta-74295) (Table 1) shows that sediments with scarce dateable carbon were prone to this process, and suggests that the contaminating carbonate derived from a single source.

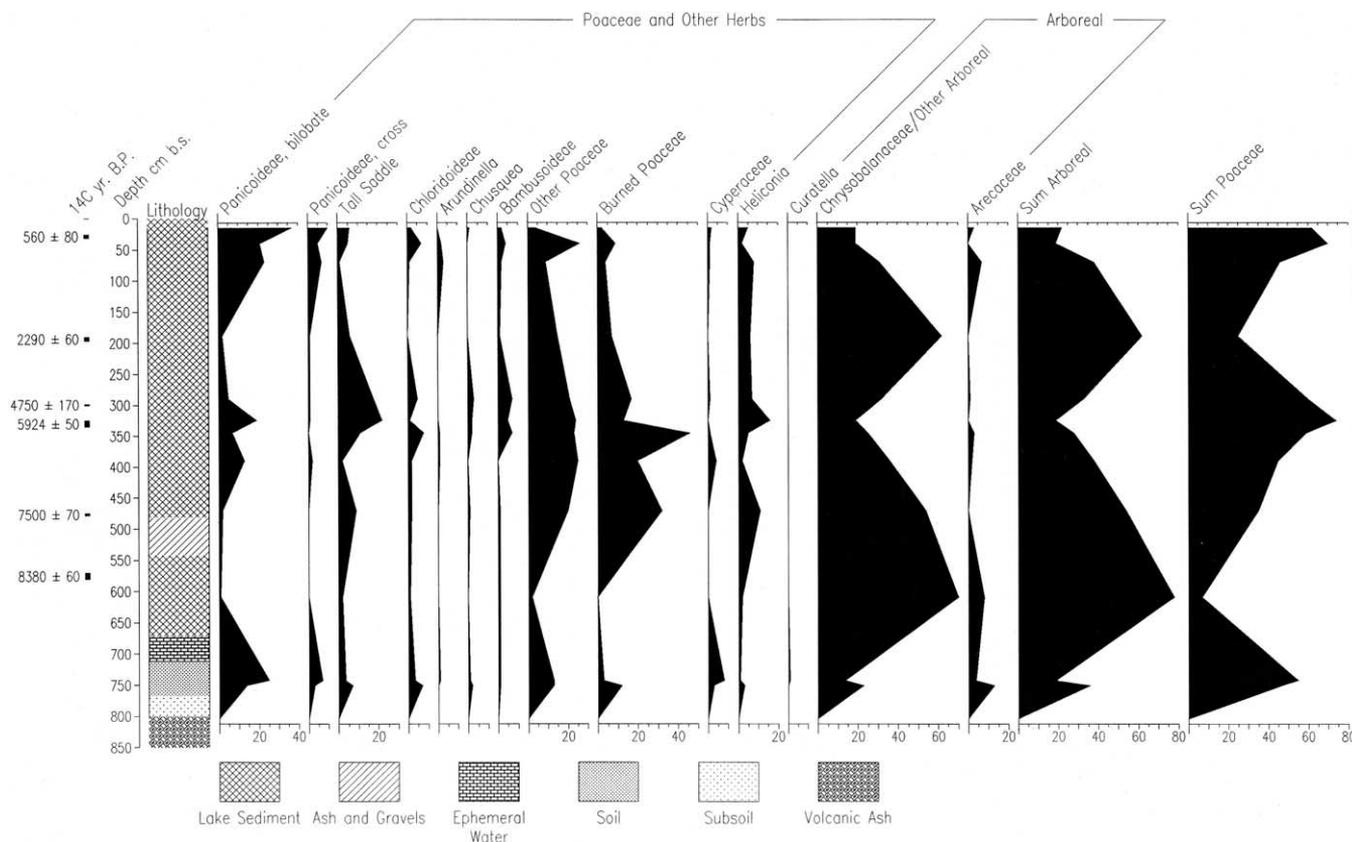


Fig. 2. Percentage data for major phytolith taxa at Monte Oscuro. Chrysobalanaceae/Other Arbooreal category contains predominantly Chrysobalanaceae phytoliths (usually > 85–90%) with contributions also from *Protium*, other Burseraceae, the Moraceae, Euphorbiaceae, Annonaceae, Connaraceae, and Flacourtiaceae. Percentages for burned Poaceae phytoliths were calculated in a separate sum. Only short cell phytoliths (e.g., bilobates, saddle-shapes) were studied for evidence of charring.

The gross stratigraphy of the core is straightforward (Fig. 2). Between greater than 10–8 m is a zone of light brown to orange-yellow volcanic ash that records the last major volcanic eruption at the crater. From 8 to 7.1 m is a soil profile characterized by a dark brown, gravelly subsoil (8–7.6 m), which is overlain by a medium to dark brown, gravelly soil with pebbles up to 3 cm in diameter (7.6–7.1 m). The interior of the crater was dry during this interval and landform conditions were stable enough to permit the development of a deep soil and associated vegetation. Between depths of 7.1 and 6.7 m, sediments are medium brown fine silts intercalated with gray, orange, and mostly black dark bands. A few small CaCO_3 clasts are present. The basin was still dry most of the time, but may have held water intermittently. Initial ponding leading to the establishment of a permanent water body is recorded between 6.71 and 6.1 m, with the deposition of a medium gray, banded, lacustrine sediment. This is the first significant zone of CaCO_3 accumulation. There is no geological limestone in this region of Panama. Penetrations of brackish water into the coring area during high sea-level stands, together with seasonal and longer-term shifts in the water table, can explain carbonate presence and movement in the sediment profile. Any effect

on sediment age caused by a marine reservoir effect should be no more than 400 years.

An estimated date for the bottom of this zone and permanent ponding at Monte Oscuro is ca. 10,500 ^{14}C yr B.P., based on an average sedimentation rate of 0.64 mm/yr calculated for the sequence. It is thus very likely that the formation of the paleosol between 8 and 7.1 m dates to late in the Pleistocene. Above 6.1 m to the top of the core is a continuous series of banded, lacustrine sediments characterized by dark brown to dark black, silty clay with bands of charcoal and occasional CaCO_3 clasts, the sediments becoming darker and the clasts fewer with decreasing depth, and broken only by a zone of ash and gravels between 5.4 and 4.8 meters.

Results

Pollen is not preserved in the paleosol, but phytoliths are well-represented. Two phytolith samples taken from depths of 7.50–7.58 m and 7.42–7.50 m indicate that the vegetation was dominated by grasses and other herbaceous taxa and contained few trees (Fig. 2). Percentages of Poaceae are

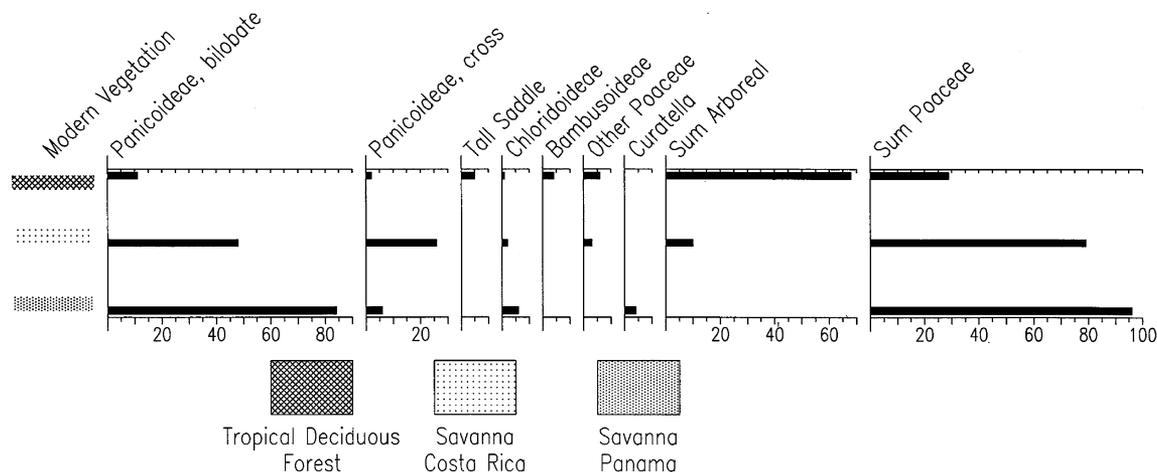


Fig. 3. Modern phytolith spectra from tropical deciduous forest in Costa Rica and derived savanna in Costa Rica and Panama. Phytolith frequencies for each habitat are averages from a series of soil transects, and represent pinch samples taken from the upper soil surface directly underneath existing vegetation.

high, the Cyperaceae reach their maximum levels of the sequence, and phytoliths from the shrub or small tree *Curatella americana*, a major indicator taxon for savanna in the Neotropics, are restricted to this segment of the core. Phytoliths from *Arundinella* spp., today tall grasses of open, windswept landscapes, occur, along with phytoliths from *Heliconia* spp., herbs of dry, open habitats. Phytoliths from the panicoid (tall grass) and chloridoid (short grass) sub-families of the Poaceae are conspicuous. All chloridoid and most panicoid grasses use the C_4 photosynthetic pathway (Kellogg, 2000). Fire occurrence is indicated by the presence of charcoal (not shown) and burned grass phytoliths. No siliceous microfossils from aquatic organisms such as sponge spicules were present, further indicating that edaphic conditions peculiar to the crater floor did not contribute to the development of the open vegetation.

Arboreal phytolith taxa in the paleosol are represented mainly by the Chrysobalanaceae and Araceae, and they account for less than 40% of the phytolith sum. The morphology of the palm phytoliths is consistent with that of more xeric species that occupy dry tropical habitats (Piperno, 1988). Phytoliths from the Burseraceae (including *Protium* spp.), Annonaceae (probably including *Unonopsis* and/or *Oxandra*), and Moraceae make up less than 1% of the sum. These taxa, along with the Chrysobalanaceae and Araceae, are among the prominent families of trees that produce copious amounts of phytoliths in their leaves and fruits and achieve a significant representation in phytolith samples from modern tropical forests (Piperno, 1988, 1993). Comparisons of the paleosol phytolith spectra with those of modern phytolith analogs constructed from tropical deciduous, semievergreen, and evergreen forests and derived savannas (where tropical deciduous forests have been cleared and burned), show that phytolith assemblages like those of the paleosol with high percentages of grasses and other herbs are found only in savannas (Figs. 2, 3) (Piperno, 1988). In contrast, modern tropical deciduous forests con-

tribute phytolith assemblages in which grasses and other herbs make up less than 30% of the phytolith sum, even though the forests are adjacent to grassy areas and pastures, have broken canopies and some intrusive, grassy growth resulting from past human disturbance, and have been penetrated at ground level by fires set in the pastures.

Our evidence thus indicates that during the Pleistocene, Monte Oscuro supported open, dry-land vegetation, in which grew many grasses and other herbaceous taxa. Forest elements apparently were not entirely eliminated from the landscape but appear to have grown in low numbers. They possibly were harbored along the margins of streams that fed the lake. Thorny-scrub plant associations cannot be recognized with a phytolith record, and hence we cannot specify whether such kinds of low tree/scrub species were also present. It is probable that thorny-scrub taxa were also part of the Late Pleistocene vegetation.

Sediments deposited during the terminal Pleistocene and earliest Holocene (between about 6.70 and 6.15 m) were phytolith- and pollen-poor compared to sediments from the rest of the sequence, possibly because water levels were not yet sufficiently stable for uninterrupted sedimentation and plant fossil accumulation to take place. Nevertheless, the pollen and phytolith records show that during the first few millennia of the Holocene, a tropical deciduous forest with considerable species diversity grew in the Monte Oscuro watershed. The Holocene phytolith record starts at a depth of 6.15 m, 35 cm below the level dated at 8360 ^{14}C yr B.P. Significant changes from Pleistocene levels are recorded, and the phytolith spectrum closely resembles its modern counterpart from tropical deciduous forest (Figs. 2, 3). Arboreal phytoliths dominate the assemblage, whereas percentages of the Poaceae and Cyperaceae are greatly reduced from before. *Curatella americana* and *Arundinella* are not recorded, while phytoliths from the Marantaceae, herbs of the moist forest understory, are present. Reduction of palm phytoliths at this time is expected, since this family is not

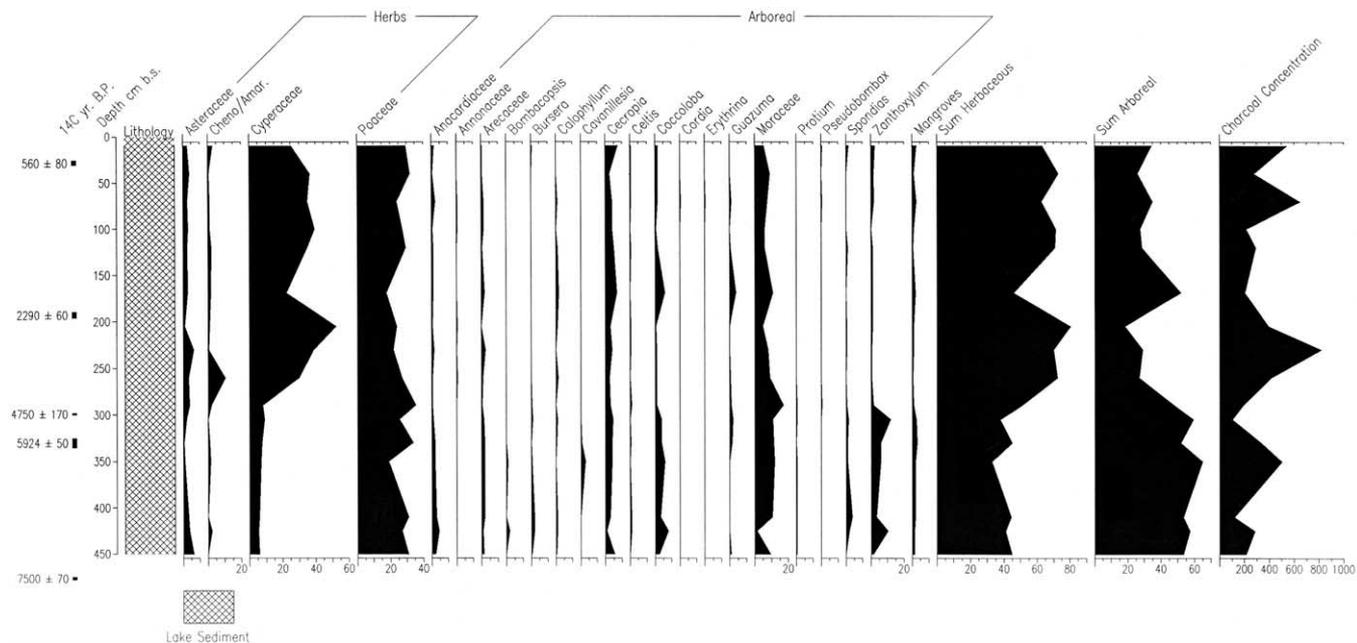


Fig. 4. Percentage data for major pollen taxa at Monte Oscuro. Charcoal concentrations are expressed in millions as number per cm^3 of sediment.

well represented in the understory and phytolith records of tropical deciduous forest (Fig. 3).

The pollen record from Monte Oscuro begins at a depth of 4.5 m, 25 cm above a level dated to 7500 ± 70 ^{14}C yr B.P. (Fig. 4). A suite of trees whose modern ecological preference is seasonal tropical forest is recorded (e.g., *Zanthoxylum*, *Spondias*, *Protium*, *Bursera*, *Erythrina*, *Celtis*, *Cavanillesia*, *Calophyllum*, *Cordia*, Anacardiaceae, Moraceae), and these and other arboreal taxa (e.g., *Trema*, *Machaerium*-type, which are not shown and account for the remainder of the pollen percentages not displayed in Fig. 4) constitute over 55% of the pollen sum. The presence of mangrove pollen (e.g., Combretaceae, *Pelliciera*, *Rhizophora*) indicates that the coast was nearby. Also recorded at this level are significant amounts of Poaceae, other taxa indicative of human disturbance (e.g., Asteraceae, Cyperaceae), and a significant rise in charcoal. In older samples, at depths between 6.8 and 5.7 m, charcoal concentrations range between 21,000 and 264,000/ cm^3 , increasing to 512,000/ cm^3 at 5.5 m. At 4.5 m, the charcoal concentration is 2.2 million per cm^3 , a very high amount. The phytolith record from 4.75 to 4.7 m also indicates an increase of vegetational disturbance including with fire, as frequencies of arboreal taxa decline, those of Poaceae rise to nearly pre-Holocene levels again, and other early successional taxa such as *Heliconia* rise sharply. Many of the Poaceae and *Heliconia* phytoliths are now charred.

These and other factors cause us to believe that the changes at 4.75 to 4.5 m most likely reflect an onset of forest modification by human populations in the Monte Oscuro watershed associated with incipient land clearance

by slash-and-burn techniques of cultivation. Small amounts of maize phytoliths are first present at 4.75 to 4.7 m. Furthermore, the morphologies of the Poaceae phytoliths are not consistent with those that would result from an increased deposition of local swamp grasses such as *Miscanthus* or *Echinochloa*, but rather appear to derive from bamboo genera such as *Guadua* spp. and other taxa adapted to forest openings. That the vegetational openings indicated by the rises in Poaceae and *Heliconia* are not those of swamps fringing the lake is also indicated by the fact that Cyperaceae pollen show no increase at this time.

Early human interference with the Panamanian forest involving the use of fire by hunters and gatherers at ca. 11,050 ^{14}C yr B.P. and significant forest clearing for slash-and-burn cultivation at ca. 7000 ^{14}C yr B.P. are indicated from the pollen, phytolith, and charcoal records at Lake La Yeguada (Piperno et al., 1990, 1991; Bush et al., 1992), located about 150 km west of Monte Oscuro (Fig. 1). Archaeological records from sites in central Panama near La Yeguada from the drainage of the Rio Santa Maria also demonstrate an early human presence and the development of horticultural systems using seed and root crops between ca. 8000 B.P. and 5000 ^{14}C yr B.P. (Fig. 1) (Cooke, 1998; Ranere and Cooke, 2002; Piperno and Pearsall, 1998; Piperno et al., 2000a,b). After ca. 7500 ^{14}C yr B.P., the Monte Oscuro pollen and phytolith frequencies are consistent with largely sustained human environmental interference and agricultural practices through time, a result concordant with paleoecological and archaeological records from other Panamanian sites (Piperno et al., 1991; Piperno and Pearsall, 1998a; Piperno et al., 2000b).

Discussion

The net effects of the competing actions of cooling, drying, and low CO₂ concentrations on Pleistocene plant communities are not well understood. Although lower atmospheric CO₂ content may have exerted a significant influence on vegetation composition and structure (Cowling and Sykes, 1999; Cowling et al., 2001), recent studies of lakes from Mexico and Guatemala show that vegetational shifts from forests to grasslands, or from C₃- to C₄-dominated ecosystems in the lowland Neotropics, are unlikely to take place without significant reductions in precipitation (Huang et al., 2001). Moreover, low CO₂ concentrations acting independent of significant climatic influences probably cannot account for the fact that many lakes from Guatemala to southern Brazil, including Monte Oscuro, were substantially lower or completely dry during the Late Pleistocene (Ledru et al., 1998; Van der Hammen and Absy, 1994; Curtis et al., 1999). Today, the lower limit of annual precipitation generally required to support a tropical deciduous forest is about 1000 to 1200 mm (Bullock et al., 1995). Hence, a suitable estimate for precipitation reduction at Monte Oscuro during the Pleistocene seems to be on the order of at least 35%.

The underlying mechanisms that may account for significantly drier Pleistocene climates in tropical America include decreased evaporation rates over cooler ocean surfaces that resulted in less atmospheric water vapor over land masses, and intensity shifts in the annual cycle of the Intertropical Convergence Zone that were forced by orbitally driven insolation changes (Webb et al., 1997; Hodell et al., 1991; Leyden et al., 1993). The estimated timing of the filling of Monte Oscuro at ca. 10,500 ¹⁴C yr B.P. is consistent with the inundation of other lakes in tropical America that were dry or much lower during the Late Pleistocene (Ledru et al., 1998; Curtis et al., 1999).

The persistence of forests during the late Pleistocene, albeit without modern analog, has been demonstrated at several sites below 1000 m in tropical America, including three in Panama; La Yeguada, El Valle, and the Gatun Basin (Bartlett and Barghoorn, 1973; Bush and Colinvaux, 1990; Piperno et al., 1990; Bush et al., 1992) (Fig. 1). The fact that these sites are situated in high-precipitation areas (e.g., annual rainfall between ca. 3000 mm and 4000 mm today) may be extremely relevant, as even under a 30% to 40% decline of precipitation sufficient moisture was probably available to support arboreal growth. This may be especially true in view of the fact that cooler Pleistocene temperatures would have improved carbon and water balance in the C₃-dominated forests by reducing evotranspiration gradients and photorespiratory carbon loss (Cowling et al., 2001). The presence of the clay type illite, which forms under conditions of limited precipitation, in the Pleistocene (ca. 14,000 to 10,500 ¹⁴C yr B.P.) but not in the Holocene deposits (10,500 ¹⁴C yr B.P. to the modern era) at Lake La Yeguada (elevation 650 m a.s.l.; annual precipitation 3800

mm a year) (Bush et al., 1992), constitutes strong evidence that this region did indeed experience a marked reduction in precipitation during the late-glacial period. In contrast to forest persistence in higher rainfall zones, forests were often displaced during the Pleistocene by savanna-like vegetation where the modern potential vegetation is a highly seasonal tropical forest (in areas with current annual precipitation between ca. 1200 and 2000 mm) (e.g., Van der Hammen and Hooghiemstra, 2000; Leyden, 1984, 1985; Van der Hammen and Absy, 1994; Pennington et al., 2000; Behling and Negrelle, 2001).

Our data from Monte Oscuro indicate that during the Late Pleistocene, the Pacific coastal plain of the Panamanian land bridge was largely a dry and open habitat. We are hesitant to use the word savanna to describe the late-glacial vegetation, because rather than the tracts of grasses and sedges dotted by low trees and shrubs characteristic of savannas today, the floristic associations may have been unusual combinations of herbaceous plants, tropical thornscrub, and temperate shrubs without modern analog (e.g., Hodell et al., 1991; Leyden et al., 1993). Our phytolith evidence also points to the presence of lowland forest trees (*Protium* spp., Annonaceae, Chrysobalanaceae, Moraceae) nearby the lake before ca. 10,500 ¹⁴C yr B.P. These taxa may have grown in low numbers in more mesic pockets on the landscape, and/or they were harbored in better-watered areas alongside water courses. In any case, the data support arguments that high postglacial dispersal rates over large distances are not required to account for early Holocene forest recovery in areas where forests were reduced (Meave and Kellman, 1994). Also, suggestions that riparian forests, whose elongated stretches of terrain can support higher levels of species diversity than previously believed, were important conservators of lowland forest trees during glacial dry periods (Meave and Kellman, 1994; Prance, 1987) may have considerable merit.

Finally, our data provide important insights into the ecological contexts of the transition from foraging to farming in Panama and other similar regions of the Neotropics. The Monte Oscuro record adds to the body of paleoecological evidence indicating that in low-lying regions such as the Pacific coastal plain of Panama, where between 1500 and 2000 mm of annual precipitation is received today on a strongly seasonal basis, a species-rich tropical forest often was not present during the late-glacial period. Rather, such vegetation started to spread on the landscape upon the rapid onset of warmer and wetter conditions between ca. 10,800 and 10,000 ¹⁴C yr B.P. The loss of open-land habitats, coupled with the extinctions of numerous species of large, herbivorous animals and spread of tropical forest with its different sets of animal and plant resources during the early postglacial period, necessitated significant reorganizations of human subsistence, technological, and settlement strategies. Such kinds of cultural responses to the end-Pleistocene perturbations are well reflected in the early Holocene archaeological records from Panama and elsewhere in the Amer-

ican tropics (Cooke, 1998; Piperno and Pearsall, 1998a; Ranere and Cooke, 2002). Thus, as in other regions of the world, the transition from hunting and gathering to farming in the lowland Neotropical forest appears to have taken place within a context of considerable paleoenvironmental change that substantially altered resource abundance and availability, and generated significant selective pressures for changes in socio-economic systems not long after the Pleistocene ended (Zhao and Piperno, 1998; Piperno and Pearsall, 1998a; Hillman, 2001).

Acknowledgments

This work was supported by the Smithsonian Tropical Research Institute (STRI) and a grant to the STRI from the Andrew W. Mellon Foundation. We thank Anthony J. Ranere for comments on the manuscript.

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