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Pleistocene Plant Fossils in and near La Selva Biological Station, Costa Rica¹

ABSTRACT

Radiocarbon dating and ⁴⁰Ar/³⁹Ar analysis of overlying tephra indicate that plant fossil assemblages exposed by stream erosion and well construction in and near La Selva Biological Station in eastern lowland Costa Rica are Pleistocene in age. We identified plant taxa based on wood, leaves, fruits, seeds, pollen, and spores examined from three sites at ca 30 m elevation. Extrapolating from modern ranges and surface temperature lapse rates suggests paleotemperatures 2.5–3.1°C cooler than at present.

RESUMEN

Dataciones radiocarbónicas y análisis de argón (⁴⁰Ar/³⁹Ar) de la tefra sobrepuesta indican una edad Pleistocénica para las asociaciones de plantas fósiles expuestas por erosión fluvial y por la construcción de un pozo dentro y cerca de la Estación Biológica La Selva en la bajura oriental de Costa Rica. Se identificaron los táxones vegetales con base en madera, hojas, frutas, semillas, polen, y esporas de tres sitios ubicados a unos 30 m sobre el nivel de mar. Los resultados, basados en la extrapolación de los ámbitos geográficos y del gradiente vertical de la temperatura superficial modernos, sugiere paleotemperaturas 2.5–3.1°C más frescas que en el presente.

Key words: Costa Rica; fossil plants; La Selva Biological Station; paleoclimate; paleoecology; Pleistocene; pollen; spores; tropical vegetation; tropical wet forest.

WE REPORT HERE ON PLEISTOCENE PLANT FOSSIL ASSEMBLAGES exposed by stream erosion and well construction at and near La Selva Biological Station (10°26' N, 83°59' W) in the Caribbean lowlands of Costa Rica. Research within the 1536 ha tropical wet forest reserve at La Selva has had a strong botanical emphasis, and considerable data therefore exist on the modern flora and vegetation (Hartshorn & Hammel 1994, Wilbur et al. 1994). Analyses of pollen grains and charcoal fragments in swamp sediments and soils have provided information on the last few millennia of vegetation history. This includes episodes of forest clearance, maize agriculture, and widespread fires associated with pre-Columbian human activity and possible late-Holocene droughts (Horn & Sanford 1992, pers. obs.; Kennedy & Horn 1997; Kennedy 1998; Horn & Kennedy 2001). The new plant fossil assemblages we report here extend the time frame of ecological studies at La Selva into the Pleistocene, beyond the limit of radiocarbon dating. They provide a window on tropical forests in eastern Costa Rica before the arrival of humans in the Americas.

The fossils we examined are the remains of ancient forests fortuitously preserved under clay-rich volcanic deposits exposed along the Río Puerto Viejo and unearthed during well construction just outside the La Guaria annex (Fig. 1). Tree trunks over 30 cm in diameter are present at both the river and well

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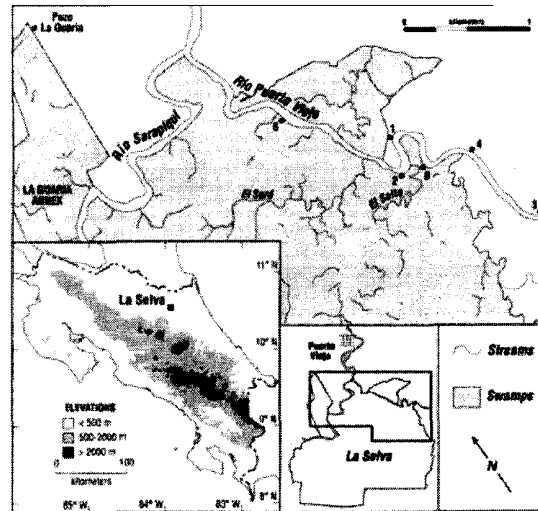


FIGURE 1. Location of the Puerto Viejo fossil exposures and Pozo La Guaria well site in and near La Selva Biological Station, Costa Rica. Map was adapted from the La Selva GIS.

sites (Fig. 2), along with other wood, leaves, fruits, seeds, pollen, and spores. Most of our samples and data come from site 1 along the Río Puerto Viejo, but we have also observed and collected plant fossils at five other locations along the river (all sites at ca 28 to 29 m elev.). One of us (RLS) first observed and collected wood exposed along the Río Puerto Viejo in 1986 (site 0); RLS and SPH examined and sampled the other sites in 1992. At the time, we were unaware that Alvarado (1990) had also examined the deposits and had obtained a radiocarbon date on a wood sample collected at or near our site 1. His sample, and three additional wood samples that we collected at sites 0, 1, and 2, all yielded ages older than the range of radiocarbon dating, i.e., older than ca 43,000 years (Table 1).

The wood at Puerto Viejo Site 1 occurs within a layer of gray, clay-rich volcanic material up to 1.4 m thick, which is in turn overlain by 11.8 m of other sedimentary deposits and the modern soil horizon at the top of the riverbank. Larger wood fragments including tree trunks are concentrated along with leaves, fruits, and seeds at the base of the gray sediment, with smaller wood fragments scattered throughout the deposit at higher levels. Excavation at site 1 showed the basal leaf layer to be up to 4 cm thick.

Based on preliminary field inspection, Alvarado (1990) described the gray sediment with plant fossils as a fluviually reworked volcanic deposit; however, laboratory examination of a sample collected at site 1 for $^{40}\text{Ar}/^{39}\text{Ar}$ analysis revealed it to be fine-grained tephra consisting of angular plagioclase crystals in a



FIGURE 2. Compressed tree trunk at Puerto Viejo site 1. Hands mark edges of trunk, now about 50 cm across. We estimate an original diameter of ca 35 cm. A smaller piece of fossil wood sits atop the trunk.

TABLE 1. Radiocarbon dates from plant fossil localities at and near La Selva Biological Station.

Lab number or reference	Sample and context	Radiocarbon age
b-54282	Charred wood from Río Puerto Viejo site 1	>45680 years BP
b-54283	Wood from Río Puerto Viejo site 2	>46350 years BP
b-54374	Wood from Río Puerto Viejo site 0	>44000 years BP
Alvarado (1990)	Wood from or near Río Puerto Viejo site 1	>43000 years BP
b-115 184	Wood from Pozo La Guaria site	>45990 years BP

dark brown bentonitic (clay) matrix. Although the matrix was altered, the texture of the feldspar grains and absence of abraded detritus indicated that the sample represents a primary airfall deposit. Whether this interpretation is true for the entire unit that includes and overlies the plant fossils will require additional field and laboratory study.

The $^{40}\text{Ar}/^{39}\text{Ar}$ analysis was performed on the coarsest plagioclase crystals (250–425 μm size fraction), which were concentrated by washing and handpicking. Altered glass adhering to the plagioclase crystals was removed by ultrasonic cleaning in dilute HF. Approximately 30 mg was irradiated for 1.5 hours along with Alder Creek (1.194 Ma) and Fish Canyon (28.02 Ma) sanidines as neutron fluence monitors, using the calibration of Renne et al. (1998). The sample was incrementally outgassed with a defocused Ar-ion laser using established methods (Renne 1995). The fine-grain size, young age, and low K content precluded single crystal analysis.

The apparent age spectrum consists of 11 steps, all of which define a plateau in the sense that the ages are mutually indistinguishable. Most of the step ages have very large errors due to the extremely small amount of radiogenic ^{40}Ar (ie., weight of the air-correction). The plateau age of 126 ± 789 ka, calculated as the inverse variance weighted mean of all step ages, is dominated by two steps that released ca 30 percent of the total ^{39}Ar . The Ca/K spectrum, determined from $^{37}\text{Ar}/^{39}\text{Ar}$, increases dramatically in the first 10 percent of ^{39}Ar released to a plateau value of 10 to 13. This high Ca/K ratio poses additional difficulties in obtaining precise data due to influence of the Ca correction (Dalrymple et al. 1981). The initially low values of Ca/K suggest the possibility of minor grain marginal alteration to K-rich clays, but this effect is not reflected in the higher temperature data that contribute most precisely to the plateau age.

Though relatively imprecise, the data show that the sample is less than 915 ka (915,000 years old) at the level of one standard deviation. Since multigrain pyroclastic samples are always potentially contaminated with xenocrysts, 915 ka is truly a maximum age. This age, in conjunction with the radiocarbon dates, establishes that the material was deposited sometime between 915 and 46 ka, and is thus Pleistocene in age. The maximum age of 915 ka is consistent with a K–Ar date of 1.2 ± 0.1 Ma on an andesite flow that underlies much of the La Selva reserve (Alvarado 1990). We attempted to further constrain the age of the deposit using thermoluminescence dating, but the material was insufficiently silicic to be suitable for this method (G. W. Berger, pers. comm.).

The Pozo La Guaria site was discovered during hand-excavation of a well (surface elev. ca 40 m) in April 1997. We were not present, but B. Paniagua reported that at a depth of 8.3 m, the well-digger encountered a very large tree (diam ca 1 m) with intact bark (D. B. Clark, pers. comm; P. Sollins, pers. comm.). Smaller wood fragments and fruits/seeds were also excavated, and a subsample of this material including blocks of adhering sediment was set aside for our later analysis. The deposit with macrofossils was described as dark in color, but overlying material appears to have included gray, clay-rich sediment similar to that exposed along the Río Puerto Viejo. A sample of excavated wood submitted for dating proved to be older than the range of radiocarbon dating (Table 1). The Pozo La Guaria and Puerto Viejo sites 1 and 2 may preserve material from the same volcanic event. A well dug in the late 1980s in the vicinity of La Guaria seems to have reached a similar deposit of fossil-rich, gray clay (P. Sollins, pers. comm.). Other deep excavations within the reserve have not encountered the material, including some that reached the lava flow dated by Alvarado (1990) to 1.2 ± 0.1 Ma (P. Sollins, pers. comm.). These observations indicate that the material, which could be of more than one age, has a discontinuous distribution.

TABLE 2. Plant material identified in the fossil deposit exposed along the Río Puerto Viejo. * indicates material *from* site 2 exposed on south side of river; all other material is from site 1. Taxonomy follows Wilbur et al. (1994).

Leaves/leaflets:	Pollen grains
Chrysobalanaceae (Parinari)	Aquifoliaceae (Ilex)
Fabaceae-Mimosoideae (tribe Ingeae)	Asteraceae
Lauraceae (Nectandra, Ocotea)	Begoniaceae (Begonia)
Piperaceae	Betulaceae (Alnus)
Sapotaceae (Pouteria)	Bombacaceae
Fruits/seeds	Cecropiaceae (Cecropia)
Annonaceae (Xylopia)	Chloranthaceae (Hedyosmum)
Arecaceae (Astrocaryum)	Cunoniaceae (Weinmannia)
Chrysobalanaceae (Parinari)	Cyperaceae
Fabaceae-Mimosoideae (tribe Ingeae)	Ericaceae
Humiriaceae (Sacoglottis)	Euphorbiaceae (Acalypha, Alchornea)
Malpighiaceae (Byrsonima)	Malpighiaceae (Heteropteris)
Menispermaceae (Abuta)	Melastomataceae/Combretaceae
Sapotaceae (Pouteria)	Myricaceae (Myrica)
Wood	Poaceae
Bignoniaceae (Jacaranda, Tabebuia)	Polygalaceae (Polygala)
Combretaceae (Terminalia)	Piperaceae (Piper)
Fabaceae-Mimosoideae (Inga or Stryphnodendron; *Inga, Stryphnodendron, or Pithecellobium)	Sapotaceae
Lauraceae (Nectandra or Ocotea)	Urticales
Sapotaceae (Pouteria)	Vochysiaceae (Vochysia)
Ulmaceae (Trema)	Fern spores
	Cyatheaceae (Cyathea, Cnemidaria)
	Polypodiaceae
	Selaginellaceae (Selaginella)
	Other fern spores

Tables 2 and 3 list plant taxa identified from leaves, fruits, seeds, wood, pollen, and spores in the Puerto Viejo and Pozo La Guaria deposits. A few macrofossils were identified in the field by authors RLS and OV, but most data reported here are derived from laboratory study of fossil leaves, fruits, and seeds by DD and TAL with assistance from OV; of fossil wood by MCW; and of fossil pollen and spores by SPH and DAC. Fossil leaf material collected at Puerto Viejo site 1 was washed with commercial detergent to separate the leaves and remove debris, then soaked in HF to remove silicates. Over 100 cuticles and whole-mount mesofossil slides of fossil leaves, and specimens of modern leaves from over 100 species, were prepared and examined to identify fossil leaves in the deposit.

Wood samples were not silicified, and it was possible to cut smooth surfaces and make hand-sections with a razor blade. In a few cases, the samples were too degraded and crumbly to prepare adequate

TABLE 3. Plant material identified in the Pozo La Guaria deposit. Taxonomy follows Wilbur et al. (1994).

Fruits/seeds:	Pollen grains
Arecaceae (Astrocaryum)	Arecaceae
Humiriaceae (Humiriastrum, Sacoglottis)	Asteraceae
Fern spores	Cecropiaceae (Cecropia)
Cyatheaceae (Cnemidaria)	Cyperaceae
Other fern spores	Ericaceae
	Euphorbiaceae (Acalypha)
	Melastomataceae/Combretaceae
	Myricaceae (Myrica)
	Poaceae
	Rutaceae (Zanthoxylum)
	Sapindaceae
	Scrophulariaceae
	Ulmaceae (Celtis, Trema)
	Verbenaceae (Ilex)

sections. For the intact samples, cross, radial, and tangential sections were prepared and mounted on glass slides for microscopic examination. Macroscopic anatomy was observed using a 10x hand lens on smoothed surfaces, and microscopic anatomy (size and arrangement of vessels, rays, and axial parenchyma) was observed using a compound microscope. A list of potential identifications was generated using the computerized GUESS wood identification program (Wheeler et al. 1986). These were compared with authentic specimens to verify genus.

Pollen and spores were prepared for microscopic analysis using standard palynological procedures (HCl, HF, KOH, acetolysis; Berglund 1986), and identified based on an extensive reference collection of tropical taxa.

If our interpretation of a primary ashfall is correct, the plant taxa identified from macrofossils exposed along the Puerto Viejo represent plants that were growing at or near the collection sites at the time of burial; however, if the deposit includes fluviially transported volcanic sediment (Alvarado 1990), it may also include plant fossils transported from upslope forests. The distribution of macrofossils within the volcanic deposit at site 1, and the presence of some charred wood at its base, is suggestive of a forest buried in place (Fritz 1986), but more detailed taphonomic and geological studies would be required to establish this. For the Pozo La Guaria samples, we have less information on sample context and cannot rule out some downslope movement of macrofossils in a stream or volcanic flow.

Given the possibility of downslope transport, it is interesting to note that all but two taxa identified from macrofossils are found within modern forests of the La Selva Biological Station (Wilbur et al. 1994). The fossils of *Parinari* (Chrysobalanaceae) found at Puerto Viejo site 1 and *Humiriastrum* (Humiriaceae) found at Pozo La Guaria are outside the modern ranges of the genera. The online taxonomic database for Costa Rica's Instituto Nacional de Biodiversidad (<http://www.inbio.ac.cr/bims/k03.htm>) and the Vascular Tropicos database of the Missouri Botanical Garden (<http://mobot.mobot.org/W3T/Search/vast.html>) indicate a modern lower elevational limit for *Parinari* (*P. excelsa* or *P. parvifolia*) on the Caribbean slope of 500 m. *Humiriastrum* (represented by one species, *H. diguense*) has been collected only above 200 m on the Caribbean slope.

The La Selva checklist (Wilbur et al. 1994) lists one taxon identified from macrofossils (*Byrsonima*) as a cultivated species. Although more often associated with drier habitats of the Pacific slope, *Byrsonima* can be a natural component of wetter forests (Anderson 1983). Several large specimens of *B. crassifolia* occur today along the Río Puerto Viejo, quite likely having established naturally, and *B. crispa* has been collected in primary premontane wet forest at 1000 m elevation on the Caribbean slope (INBIO database).

While microfossils (pollen and spores) can be carried long distances by wind, our previous studies of pollen in surface soils at La Selva (Horn et al. 1998) and elsewhere in Costa Rica (Rodgers & Horn 1996) indicate that soil pollen spectra within forests are to a large degree dominated by the pollen of local plants. If the Puerto Viejo and Pozo La Guaria macrofossil assemblages represent ancient forests buried in place, the associated pollen and spore assemblages should primarily reflect the plants that once grew at the sites. If macrofossils were transported downslope, however, microfossils may also have been transported.

As is true for the plant macrofossils, most of the pollen and spores at the Puerto Viejo and Pozo La Guaria sites represent plant taxa in the modern La Selva flora (based on Wilbur et al. 1994, with additional information on tree ferns from Gómez 1983). Three genera represented by fossil pollen (*Alnus*, *Myrica*, and *Weinmannia*) do not grow at La Selva today. These wind-pollinated trees and shrubs are presently restricted to premontane and montane forests growing ca. 500–1000m or more upslope from La Selva (Horn & Rodgers 1996–1997, Burger 1977, and online databases cited above). Together, these three genera account for 9 percent of the total pollen enumerated in five samples prepared from sediment associated with site 1 macrofossils. This percentage of “extralocal” pollen is higher than we have found under modern closed forest canopies at La Selva (Horn et al. 1998; S. Horn, pers. obs.), but is similar to pollen percentages in surface and recent samples from the open-canopy Cantarrana swamp (Kennedy 1998), which receives pollen from upslope plant communities carried by downslope winds. The importance of premontane/montane pollen types in the Puerto Viejo and Pozo La Guaria sediments is consistent with the presence of macrofossils of two genera presently found only upslope from La Selva. Because of the potential for long-distance wind dispersal of pollen, the plant macrofossils, which are generally dis-

tributed short distances (Roth & Dilcher 1978), provide the stronger evidence for differing plant distributions in the past.

If the Puerto Viejo and Pozo La Guaria fossil assemblages represent ancient forests buried in place, the presence of *Humiriastrum* and *Parinari* macrofossils at ca 30 m elevation suggests downslope range extensions (relative to the present) of at least 170 and 470 m, respectively. If we envision such range extensions as primarily reflecting lower temperatures and apply a modern surface temperature lapse rate of 5.4° C/km (Orvis & Horn 2000), the fossil finds of *Parinari* yield an estimated paleotemperature at least 2.5°C cooler than at present. The modern elevational ranges of other taxa represented in the fossil assemblages, as recorded in the INBIO and VAST databases cited above, and by Chazdon (1987) for palms, reveal that such a temperature depression could be accommodated by all other components of the macrofossil assemblages, which include no narrowly distributed lowland taxa that would be "pinched out" by such cooling; however, several taxa in the macrofossil assemblages reach their modern upper elevational limits between 600 and 800 m, constraining the extent of possible cooling. The palm *Astrocaryum*, identified from fruits/seeds in both the Puerto Viejo and Pozo La Guaria material, extends as high as ca 600 m on the Caribbean slope (Chazdon 1987). *Sacoglottis*, also identified from fruits/seeds at both sites, has been collected only as high as 500 m on the Caribbean slope of Costa Rica; however, it is common at elevations up to 600 m on Cocos Island and has been collected above 800 m elevation on the Caribbean slope of central Panama (VAST database). The genus *Tabebuia*, identified from wood at Puerto Viejo site 1, presently reaches its upper elevational limit on the Caribbean slope at 675 m, while *Parinari* reaches its upper limit at 770 m. *Stryphnodendron*, a possible match for wood samples at Puerto Viejo sites 1 and 2, reaches its upper elevational limit at 750 m. To accommodate the modern ranges of these taxa would require cooling of no more than 3.1°C (calculated from the upper limit of *Astrocaryum*).

Paleotemperatures 2.5–3.1°C cooler than at present could explain the absence of macrofossils or pollen of *Pentaclethra maculosa* in our samples. This leguminous tree has an elevational range in eastern Costa Rica from sea level to only ca 500 m (Hartshorn 1983, INBIO database). The species is particularly common at La Selva, where it dominates old alluvial soil, residual soils, and forested swamps, and commonly shows importance values (percent frequency + percent density + percent basal area/3) twice those of the next most important species (Hartshorn 1983). Its leaflets are abundant in litter samples and its pollen is large, distinctive, and well represented in swamp sediments at La Selva (Rodgers & Horn 1996, Kennedy 1998). While it is dangerous to make interpretations based on the absence of evidence, *P. maculosa* would be hard to miss in either macrofossil or microfossil samples. The fact that it is absent in our Pleistocene fossil samples may indicate an unsuitably cool paleoclimate.

We note that the magnitude of cooling hypothesized is much less than the cooling calculated to have occurred during the maximum extents of the last three major glacial advances recorded in Valle de las Morrenas on the Chirripó massif of the Cordillera de Talamanca (Orvis & Horn 2000). Reconstructions from moraines and trimlines in this valley on the north side of Costa Rica's highest mountain peak indicate maximum ice extents were reached at times when temperatures were 7.4–7.8°C below modern temperatures. Extrapolating to the lowlands using present-day surface lapse rates, contemporary climates at La Selva may have been similar to climates now experienced at ca 1400 m on the Caribbean slope. The composition of our fossil assemblages makes it unlikely that they grew during periods of maximum cooling and ice extent. The ancient forests may have thrived during glacial periods of less extreme cooling, transitions between glacial and interglacial or interstadial climates, or possibly even cooler portions of interglacials or interstadials. The marine isotope record (Bradley 1999) indicates that the time period between 915 and 46 ka includes ca 25 isotope stage boundaries indicating transitions between glacial and interglacial or interstadial climates, and very possibly a wealth of other periods in which climate fell somewhere between the warmth of the present and the extreme cooling represented by the local glacial maxima.

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Sally P. Horn²

Department of Geography
304 Burchfiel Geography Building
University of Tennessee
Knoxville, Tennessee 37996, U.S.A.

Robert L. Sanford Jr.

Department of Biological Sciences
University of Denver
Denver, Colorado 80208, USA.

David Dilcher, Terry A. Loti

Florida Museum of Natural History
University of Florida
Gainesville, Florida 32611, U.S.A.

Paul R. Renne

Berkeley Geochronology Center
Berkeley, California 94709, U.S.A. and
Department of Earth and Planetary Science
University of California
Berkeley, California 94720, U.S.A.

Michael C. Wiemann

Center for Wood Anatomy Research
USDA Forest Service Forest Products Laboratory
Madison, Wisconsin 53705, U.S.A.

Duane Cozadd

Department of Geography
University of Tennessee
Knoxville, Tennessee 37996, U.S.A.

and

Orlando Vargas³

La Selva Biological Station
Organization for Tropical Studies
Puerto Viejo de Sarapiquí, Costa Rica

² Corresponding author. e-mail: shorn@utk.edu; Telephone: 865-974-6030.

³ Current address: Reserva Ecológica Bijagual de Sarapiquí, Apartado 35-3069, Costa Rica.
