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## Prehistoric Maize Cultivation at the La Selva Biological Station, Costa Rica<sup>1</sup>

*Key words:* agriculture, Costa Rica, La Selva Biological Station, maize, preColumbian, prehistoric, *Zea mays*.

THE LA SELVA BIOLOGICAL STATION in the central Atlantic lowlands of Costa Rica (10°26'N, 83°59'W) is a key site for research on rainforest environments and biota (McDade *et al.* 1994), especially trees (Hartshorn & Hammel 1994). Biologists once considered mature forests of the reserve to be “pristine” or “virgin”—*i.e.*, undisturbed by people (Frankie *et al.* 1974, Hartshorn 1983). However, a recent archaeological survey of La Selva and its surroundings, and studies of soil charcoal and vegetation distributions, show this view to be incorrect. Quintanilla (1990) found archaeological structures and ceramic and lithic artifacts that attest to prehistoric occupation of the La Selva reserve by sedentary agricultural groups, at least between 1000 BC and 500 AD. Charcoal is abundant in soils outside of likely habitation sites (as well as within them; Quintanilla 1990), indicating the burning of surrounding forests in fires set accidentally or intentionally by preColumbian agriculturalists, or perhaps ignited by lightning (Horn & Sanford 1992 and unpubl. data). Landscape-scale analysis of palm distributions implicates later (historic) human populations as agents of forest disturbance, in this case through harvesting activities (Clark 1994, Clark *et al.* 1995).

While it now seems clear that forests at La Selva have been subjected to a long history of human disturbance, questions remain about the chronology and nature of past human activity. Here, we add to knowledge of La Selva's human history by reporting pollen evidence of prehistoric cultivation of maize (*Zea mays* L.) within the reserve. Our evidence derives from the analysis of sediment cores from swamps that we are studying to document vegetation and disturbance history at La Selva. Our results to date reveal that maize was cultivated in or near two swamps on a terrace above the Río Puerto Viejo about 700 years ago.

Most of our present data come from the ongoing analysis of a 5.9 m sediment core from the Cantarrana Swamp, a 0.2 ha, non-forested swamp located at an elevation of 36 m. Accelerator mass spectrometer (AMS) and standard radiocarbon dates on leaves, charcoal, and wood fragments in the core indicate that it spans approximately the last 3200 years. Our pollen samples were prepared using standard techniques (Berglund 1986) and mounted in silicone oil. To date we have found 18 grains of *Z. mays* pollen, all between depths of 104–224 cm in the core. We first discovered the maize pollen during our standard pollen counts, conducted using light microscopy at 400x magnification. To check for additional occurrences of maize, we prepared and scanned at lower magnification (100x) one to several slides from each of 63 levels in the core.

We have also found maize pollen (2 grains) at 232 cm in an undated sediment core from a second swamp at La Selva. The Machita Swamp (unofficial name) is located at the head of the Quebrada Leonel, approximately 2 km west of the Cantarrana Swamp on the same alluvial terrace (Sollins *et al.* 1994). The 232 cm sample in which we found the maize pollen is the only sample that we have examined thus far from the Machita core.

Grains of *Zea* pollen in the Cantarrana and Machita sediments are 64–79  $\mu\text{m}$  in diameter with pores 10–14  $\mu\text{m}$  in diameter. These dimensions are within the size ranges of modern and archaeological samples of maize pollen from Mexico and Central America (Ludlow-Wiechers *et al.* 1983). Many of the samples that contain maize pollen also contain microscopic and/or macroscopic charcoal, indicating fires likely associated with maize cultivation.

The lowest occurrence of maize in the Cantarrana core is one cm below the depth from which we obtained an AMS radiocarbon determination on charred wood of  $805 \pm 35$  yr BP (NOSAMS 0S-4410), which calibrates to 701 calendar years BP or 1249 AD (Stuiver & Pearson 1993). Assuming steady rates of sediment accumulation in the Cantarrana swamp over the past 700 years suggests, this result that the upper occurrence of maize pollen at 104 cm is approximately 350 years old.

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Most of the archaeological evidence presently available from La Selva, as well as that for surrounding areas of the cantón of Sarapiquí (Quintanilla 1990) is associated with the regional archaeological phase known as the El Bosque phase (300 BC to 500 AD), which was a time of explosive population growth in the Atlantic lowlands of Costa Rica (Snarskis 1981, 1984). Although later archaeological periods are represented at sites near La Selva (Gutierrez & Mora 1988, Quintanilla 1990), no artifacts diagnostic of later phases have been found within the boundaries of the La Selva reserve. Our discovery in the Cantarrana swamp of maize pollen in association with 700-year-old charcoal thus extends the known period of human occupation of La Selva, in this case to the much later La Cabaña phase (1000 AD to 1550 AD); the latter is associated with the highly organized caciques or chieftains who ruled eastern Costa Rica until the arrival of the Spaniards in the 16th century (Snarskis 1981, 1984). Our pollen evidence from the Cantarrana swamp also provides the first direct botanical evidence of prehistoric agricultural activities within the La Selva reserve.

The evidence of maize cultivation at La Selva during the La Cabaña phase is consistent with present understanding of the regional history of maize, which is believed to have surpassed manioc (*Manihot esculenta*) in dietary importance in the Atlantic lowlands by the beginning of the El Bosque phase more than a millennium earlier (Snarskis 1984). While we have yet to discover botanical evidence of maize in El Bosque age sediments or sites at La Selva, lake sediment cores from our paleoecological sites elsewhere in the Atlantic lowlands contain maize pollen that dates to the El Bosque phase or slightly earlier (Northrop & Horn 1996, Horn & Rodgers unpubl. data). Also, a maize cob was recovered at the El Bosque phase Severo Ledesma archaeological site near Guácimo some 45 km southeast of La Selva (Snarskis 1981). Macrofossils of maize are also known from later archaeological sites in the central Atlantic lowlands (Snarskis 1984, Blanco & Mora 1994).

The development of AMS radiocarbon dating has made possible the dating of individual seeds and other very small organics; this ability, coupled with the increased use of flotation recovery at archaeological sites and advances in scanning electron microscopy, has led to the application of more exacting standards to evidence of the history of domesticated plants in North and South America and consequent reevaluation of the chronologies of several crop plants, including maize (Smith 1994–95, Fritz 1994). Our maize pollen evidence from La Selva, and much or all evidence of prehistoric maize in Costa Rica, falls short of attaining “first category” status, which is reserved for seeds or other plant parts that exhibit morphologies associated with deliberate planting and harvesting, and that are directly dated using the AMS method. The maize pollen grains from La Selva have not been directly dated (and are insufficiently concentrated in the sediment to allow such dating); in the scheme of Smith (1994–95) they constitute “second category” evidence and are therefore potentially suspect (Smith 1994–95; see also Fritz 1994). However, while our maize pollen grains do not meet Smith’s most exacting standards, they do not create chronological controversies, as do for example maize pollen and phytoliths from the Amazon, which predate maize macrofossils by several millennia (Smith 1994–95). Rather, the La Cabaña age maize pollen from La Selva, as well as earlier maize microfossils and macrofossils from the central Atlantic watershed, are consistent with the conservative view derived from directly dated macrobotanical evidence that maize was domesticated in Middle America between 5500 and 5000 BP, and appeared in Tehuacán by 4700 BP, on the Gulf and southern Pacific coasts of Mexico by about 3400 BP, and in South America by 3200–3000 BP (Smith 1994–95).

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## Parasitic Phorid Flies: A Previously Unrecognized Cost to Aggregation Behavior of Male Stingless Bees<sup>1</sup>

*Key words:* Apidae, lek, parasitoid, Phoridae.

AGGREGATIONS OF MALE INSECTS for mating purposes are a common phenomenon. In some situations these concentrations give females greater control over their choice of mates, based on their observations of characters that presumably indicate increased fitness, such as the position of males in a swarm (Thornhill & Alcock 1983). Other aggregations are at places where females are known to occur frequently, such as at feeding sites. All such aggregations, however, expose males to greatly increased levels of predation and parasitism (references in Thornhill & Alcock 1983). This is especially true of phorid flies (Diptera: Phoridae), which are well-known to attack hosts in aggregations (Borgmeier 1937; Feener 1981, 1987,

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