ics (*30–32*). Mean annual rainfall on the Yucatan Peninsula varies by a factor of 5 over a distance of only ~500 km between the semiarid northwest coast (500 mm/year) and the southern lowlands of northern Guatemala and Belize (2500 mm/year) (Fig. 1). Consequently, any solar-forced change in the strength or position of Hadley circulation or tropical convective activity would be expected to affect rainfall in the region.

A comparison of the Chichancanab GRA bulk density record with bandpass filters of the signal, centered at periods of 50 and 208 years, shows that the large bicentennial-scale drought events were often composed of multiple ~50-year oscillations. The record demonstrates that the arid events centered at 485 B.C. and 285 B.C. were part of the 208-year cycle (Fig. 5). Similarly, the droughts between 125 and 210 A.D. (associated with Preclassic Abandonment), at ~800 A.D. (associated with terminal Classic Collapse), and ~1020 A.D. also fit the pattern of 208-year drought recurrence. The Maya were highly dependent on rainfall and surface reservoirs as their principal water supply (*15*). Consequently, these multidecadal- to multicentury-scale oscillations in precipitation probably had a detrimental impact on Maya food production and culture.

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Origin and Environmental Setting of Ancient Agriculture in the Lowlands of Mesoamerica

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Archaeological research in the Gulf Coast of Tabasco reveals the earliest record of maize cultivation in Mexico. The first farmers settled along beach ridges and lagoons of the Grijalva River delta. Pollen from cultivated *Zea* appears with evidence of forest clearing about 5100 calendar years B.C. (yr B.C.) [6200 ^{14}C years before the present (yr B.P.)]. Large *Zea* sp. pollen, typical of domesticated maize (*Zea mays*), appears about 5000 calendar yr B.C. (6000 yr B.P.). A *Manihot* sp. pollen grain dated to 4600 calendar yr B.C. (5800 yr B.P.) may be from domesticated manioc. About 2500 calendar yr B.C. (4000 yr B.P.), domesticated sunflower seeds and cotton pollen appear as farming expanded.

Mesoamerica is one of the cultural regions of the world that served as a cradle for plant domestication. Early research on plant domestication focused on the semi-arid highlands of Mexico, where preservation of plant macrofossils in dry caves was optimal (*1*, *2*). The rich paleoethnobotanical data recovered from caves formed the basis for the hypothesis that the highland region was the center of domestication in Mesoamerica. Evidence for early agriculture has been more difficult to find in the lowlands, where humid conditions typically lead to poor plant preservation. Thus, the role of the humid tropical areas of Mesoamerica in plant domestication has remained terra incognita, although this region gave rise to one of the New World's first complex societies: the Gulf coast Olmec circa (ca.). 1300 calendar yr B.C. (*3*).

Our research traces the interaction of early lowland farmers with their dynamic coastal lagoon and estuarine environment in the Gulf coast of Mexico. Fieldwork focused on the small site of San Andrés (Fig. 1), located 15 km south of the Gulf of Mexico and 5 km northeast of the major Middle Formative Olmec center of La Venta in western Tabasco, Mexico (*4*). This part of Tabasco is hot and humid, with a marked seasonality in rainfall [a total of 800 mm from September to October, versus a total of 200 mm from January to May (*5*)]. The ecology and geomorphology of the coastal zone are characterized by mangroves bordering bar-

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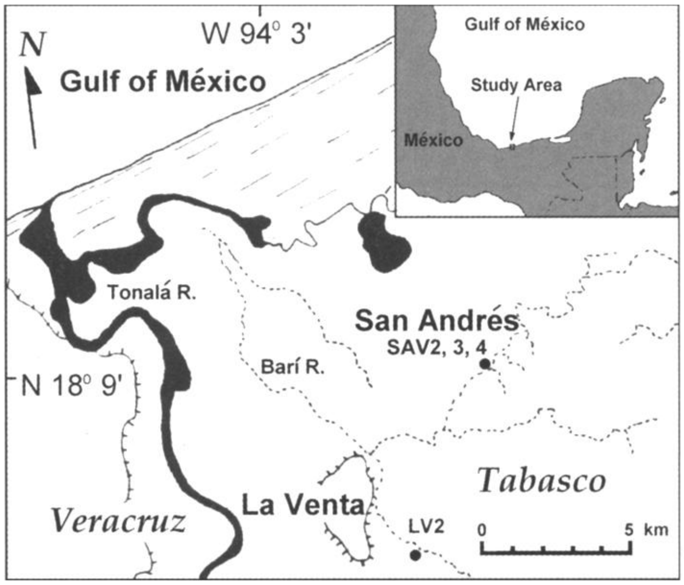
rier beaches, lagoons, and estuaries of the Grijalva River delta (*5*). We selected San Andrés for study on the basis of traces of an early (ca. 2000 calendar yr B.C.) occupation that included the cultivation of maize (*6*). We built on methods developed in our earlier research in northern Belize (*7*), combining data from the sediment cores with data from the adjacent wetland excavations (Fig. 2). Excavations at San Andrés extended well below the modern water table. In contrast to most tropical zones, the preservation of macro- and microbotanical remains is excellent in these waterlogged soils. We wet-screened most of the excavated earth using a fine (3-mm) mesh screen. Soil samples from each 20-cm level and all cultural features were processed by flotation. We acquired four sediment cores using a gasoline-powered vibracore and a 3-inch aluminum pipe (Fig. 2). Pollen from the four cores was analyzed with a Jenaval compound stereomicroscope at magnifications of 400 to 1200× and with a Nikon Optiphot microscope at 1000× with Nomarski Phase interference. Core sediments were sampled in 5-cm increments, and a minimum of 200 pollen grains was counted for each sample. The remainder of the slide was visually scanned for additional cultigens. Seventeen additional slides were prepared from the SAV3 core, and the entire slide was scanned for the presence of cultigens. The diameters and pores of 82 *Zea* sp. grains were measured at both 400 and 1000× magnification. Radiocarbon dating of organic material from the cores and excavations, coupled with stratigraphic correlations, provide a chronology for environmental and cultural change (Table 1 and Fig. 2).

The paleoecological data indicate that from ca. 4300 to 3400 calendar yr B.C., a large barrier lagoon extended from La Venta to San Andrés, evidenced by deposits of silt and clay with oysters (*Ostrea* sp.), peat fragments, and abundant red mangrove (*Rhizophora mangle*) pollen found in all four cores [SAV2, 3, 4, and LV2 (Fig. 2)]. The lagoon deposits overlie and

Fig. 1. Map showing the location of the Olmec center of La Venta and the adjacent study site of San Andrés. Indicated are cores SAV2, 3, 4, and LV2 and the ancient channel of the Barí River (dashed line). Hatched lines demark boundaries between the Grijalva deltaic plain of Tabasco and the Tertiary hills found in Veracruz and at La Venta. The map is based on Landsat Thematic Mapper satellite imagery.



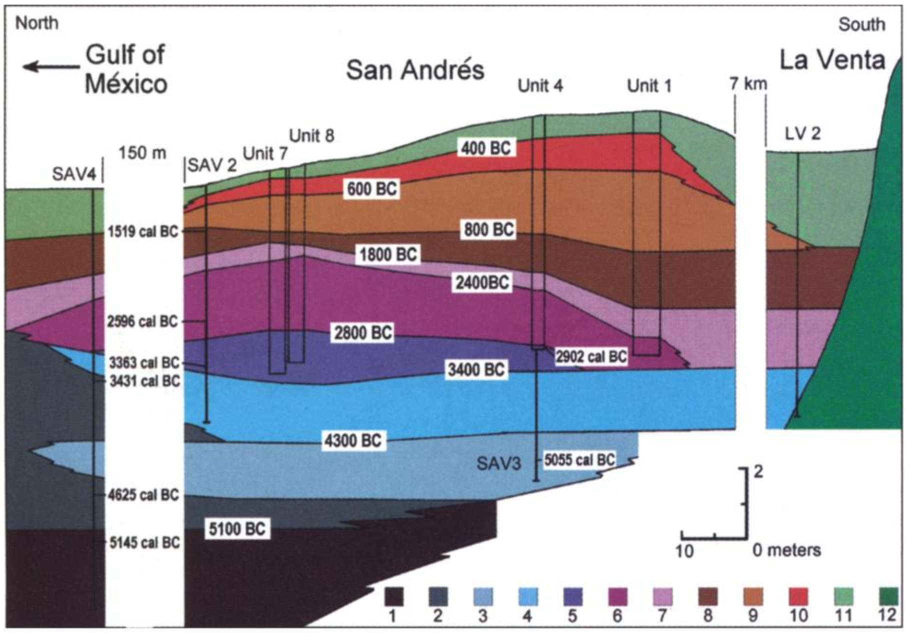


Fig. 2. Stratigraphy of San Andrés, Tabasco. Shown are calibrated radiocarbon intercept dates (calendar yr B.C.) and approximate ages of stratigraphic boundaries (Table 1). Key: 1, Early Holocene estuary; 2, laminated fine sand and clay of beach washover deposit; 3, fine sand of beach washover deposit; 4, lagoon silts and clays; 5, estuarine sandy loam; 6, estuarine silty loam; 7, marsh organic-rich silts and clays; 8, swamp peat and peaty clay; 9, Barí River levee loam; 10, Olmec cultural deposit; 11, recent alluvium and undifferentiated sediments; 12, Tertiary bedrock overlying the La Venta salt dome. Note the vertical exaggeration (5×).

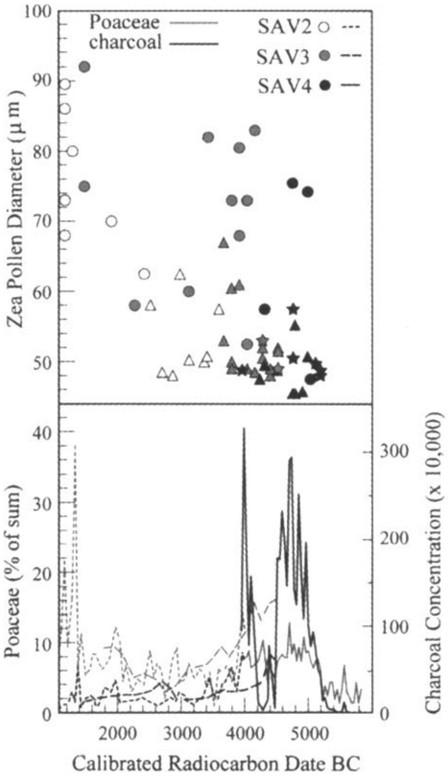


Fig. 3. Selected pollen and charcoal data from the SAV2, 3, and 4 cores. Dates are based on linear regression of depth versus age for stratigraphically consistent calibration intercept dates from SAV2, 3, and 4 (Table 1). Charcoal concentrations are per cubic centimeter for particles ranging from 8 to 80 μm in diameter. *Zea* sp. pollen grains with major axis/pore diameter ratios (PDs) of 3.8 to 3.9 are shown as stars, PDs of 4.0 to 4.9 are shown as triangles; and PDs of 5.0 to 6.1 are shown as circles. *Zea* sp. grains >70 μm in diameter and with PDs ≥ 5 are probably from domesticated maize. The percentage of Poaceae (grass) pollen is shown as an indicator of land disturbance. There is an abrupt rise in charcoal and Poaceae pollen with the first appearance of *Zea* sp. pollen.

interfinger with beach sands in SAV3 and SAV4, which overlie an early Holocene estuary deposit in SAV4. The laminated fine sands and clays in SAV4 are typical of lagoon washover deposits that form behind a barrier beach, and thus confirm that the ancient beach ridge lies just north of the core site. These washover deposits formed between 5100 to 4300 calendar yr B.C. and mark the maximum postglacial marine transgression and the first barrier beach-lagoon system in the area.

Pollen grains of the genus *Zea* first appear in the SAV4 core ca. 5100 calendar yr B.C. (Figs. 3 and 4A). The earliest grain sizes (48.0 to 49.8 μm) and major axis/pore ratios (3.8 to 3.9) fall within or near the ranges of 46.4 to 87.0 μm and 3.9 to 9.4 established by Whitehead and Langham (*8*) for wild *Zea* (teosinte). Under Nomarski phase interference, these grains exhibit distinctive intertectile columella (*8*), which are characteristic of *Zea* grains. *Zea* sp. grains larger than 70 μm first appear ca. 5000 calendar yr B.C., and by 4000 calendar yr B.C., they are common (Fig. 3). These larger grains (Fig. 4B) have sizes (74 to 92 μm) and major axis/pore ratios (5.0 to 6.1) typical of domesticated maize (*Zea mays*) (*8*). These grains also have the distinctive columella characteristic of *Zea*.

The earliest *Zea* sp. pollen at San Andrés (ca. 5100 calendar yr B.C.) represents exotic plants introduced and cultivated by farmers on the barrier beach. No wild species of *Zea* are native to coastal Tabasco (*9*). The appearance of small *Zea* pollen coincides with the initial period of forest clearing, evidenced by charcoal and disturbance pollen such as that from grasses of the family Poaceae (Fig. 3). Large, probable domesticated maize pollen appears only about 100 years later, and by 4800 calendar yr B.C. extensive land clearing and maize cultivation were under way. The settlement at San Andrés is linked to the formation of the beach ridge and lagoon system, which attracted maize farmers to the area because of the combination of tillable soils and aquatic resources.

The small *Zea* sp. pollen was abundant for over 2500 years, finally disappearing about 2500 calendar yr B.C. We do not know, however, whether this extreme range in *Zea* sp. pollen grain size and morphology represents variability within a single taxon, perhaps under the selective pressure of cultivation, or cultivation of more than one variety of *Zea*. Early maize cobs from highland Mexico exhibit evidence of rapid evolutionary change and a high degree of variability in cob morphology from

Table 1. Radiocarbon dates from San Andrés and La Venta, Tabasco, Mexico. Depths below each datum are given in centimeters after the core name (e.g., SAV2), the auger test (Auger26), or the San Andrés excavation number (e.g., Unit1). The calibration to calendar date is from the Calib 4.2 program (*18*). Where more than one calibration curve intercept occurs, the center date is given.

Sample	^{14}C age (yr. B.P.)	Calibrated date 2σ calendar yr B.C.	Calibration curve intercept (calendar yr B.C.)	Material
		River levee		
LV2–318 Beta–121636	2260 ± 160	794–AD 70	266	Sediment
Unit1–105 Beta–112668	2340 ± 90	764–182	398	Charcoal
Unit7–180 AA33577*	2345 ± 50	725–219	399	*Phaseolus* seed
Unit7–180 AA33925*	2390 ± 50	760–385	406	*Zea mays* cob
Unit7–345 Beta–122240	2420 ± 60	783–389	445	Wood
Unit7–180 AA33924*	2430 ± 35	762–401	449	*Zea mays* cob
Unit7–158 Beta–122241	2490 ± 40	792–409	636	Charcoal
Unit7–245 AA33926*	2505 ± 45	797–410	670	*Zea mays* cob
Unit1–205 Beta–112669*	2510 ± 50	800–409	671	Charcoal
LV2–252 Beta–121634*	2530 ± 50	803–412	764	Sediment
Auger26–290 AA33923*	2565 ± 45	813–542	790	*Zea mays* cob
LV2–292 Beta–121635*	2630 ± 40	885–785	802	Wood
		Freshwater swamp		
Unit1–540 Beta–106949	2950 ± 80	1405–920	1179	Charcoal
Unit1–540 Beta–112671*	3090 ± 50	1488–1135	1331	Charcoal
		Brackish swamp		
SAV2–183 Beta–106803	3250 ± 70	1688–1398	1519†	Sediment
Unit1–600 Beta–112672*	3680 ± 40	2197–1941	2101	Charcoal
Unit8–250 Beta–122242	3800 ± 70	2465–1984	2226	Charcoal
		Estuary: silty		
Unit7–265 AA33578*	3945 ± 55	2577–2288	2465	*Cionosicyos* seed
SAV2–440 Beta–106948	4080 ± 100	2894–2346	2596†	Wood
Unit7–291 AA33579*	4085 ± 50	2871–2472	2548	*Helianthus* fruit
Unit8–460 Beta–122244*	4070 ± 60	2874–2466	2613	Charcoal
Unit8–380 Beta–137882*	4130 ± 40	2878–2503	2667	*Helianthus* seed
Unit8–290 Beta–122243*	4170 ± 50	2890–2580	2773	Charcoal
		Estuary: sandy		
Unit8–480 AA33581*	4220 ± 75	3007–2580	2879	*Cucurbitaceae* seed
Unit4–625 Beta–106947	4300 ± 50	3076–2876	2902†	Charcoal
SAV2–568 Beta–106804	4600 ± 59	3515–3104	3363†	Wood
		Lagoon		
SAV4–670 AA38766*	4681 ± 67	3639–3347	3431†	Wood
SAV4–775 AA38767*	4447 ± 48	3347–2919	3095	Wood
SAV4–837 AA38768*	4513 ± 45	3365–3029	3188	Wood
LV2–710 Beta–121638*	4950 ± 50	3910–3644	3708	Wood
SAV3–830 Beta–113156*	6550 ± 90	5656–5321	5481	Sediment
		Beach washover		
SAV4–993 AA38768*	5805 ± 49	4783–4505	4625†	Wood
SAV4–1020 AA38770*	5517 ± 51	4457–4252	4348	Wood
SAV3–978 AA33582*	6140 ± 45	5258–4860	5055†	Wood
		Early Holcene estuary		
SAV4–1125 AA38771*	6208 ± 47	5301–5001	5145†	Wood

*AMS dates. †Dates used to estimate the core age-depth relationship shown in Fig. 3.

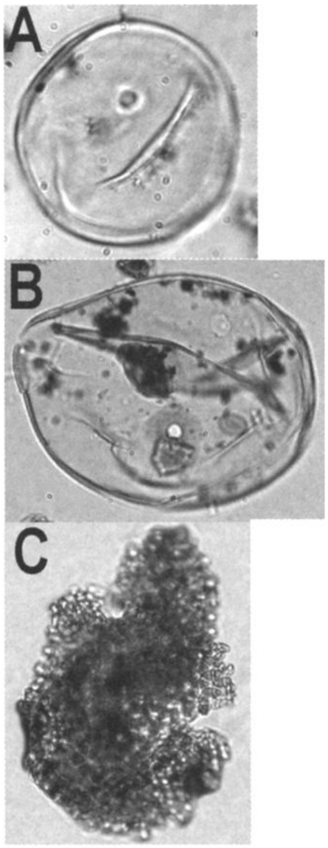


Fig. 4. Photomicrographs of pollen grains. (**A**) Small *Zea* sp. (ca. 4200 calendar yr B.C., 49 μm in diameter). (**B**) Maize (ca. 1500 calendar yr B.C., 92 μm in diameter). (**C**) *Manihot* sp. (ca. 4600 calendar yr B.C.; the maximum diameter of the fragmentary grain is 92 μm; the original grain is likely to have been in excess of 150 μm).

4300 to 3500 calendar yr B.C. (*10*), a finding that is consistent with our pollen data.

A single *Manihot* sp. pollen grain found in SAV4 dates to about 4600 calendar yr B.C. The surface morphology and large size (at least 150 µm) of the grain (Fig. 4C) indicate that it is probably from domesticated manioc (*Manihot esculentum*), although the species cannot be positively identified from the pollen. Manioc is an insect-pollinated plant, and its pollen is rare in sediments. Thus, either the discovery of *Manihot* sp. at San Andrés was fortuitous, or abundant stands of *Manihot* sp. were growing close to the site. Its occurrence correlates with the period of maximum burning and land clearance by farmers at San Andrés.

By about 3400 calendar yr B.C., the barrier beach and lagoon system had migrated northward, and the lagoon began to fill with sand, silt, and clay typical of distributary channel levees in the Grijalva deltaic system (*5*). Floral and faunal data from all excavations and cores confirm that the levee bordered a brackish estuary. Present were brackish gastropods (*Nassarius vibex* and *Nerita reclivata*), marsh clam (*Rangia cuneata*), oysters (*Ostrea* sp.), garfish (*Lepisosteus* spp.), and manatee (*Trichechus manatus*), as well as abundant red mangrove. Radiocarbon analyses (Table 1) confirm that over 3 m of estuary sediment accumulated between 3400 and 2400 calendar yr B.C..

Human activity at San Andrés continued during estuarine deposition. The fauna noted above, except the gastropods, are mostly human food refuse. Domestic dog bones (*Canis familiaris*) are also present. Seeds and rind fragments from wild plant foods of the family Cucurbitaceae were recovered, including *Cionosicyos macranthus,* which was dated by accelerator mass spectrometry (AMS) to 2465 calendar yr B.C. (intercept date). Maize pollen is common throughout the estuary horizon in the SAV2 and SAV3 cores. Near the end of this estuarine occupation, ca. 2500 calendar yr B.C., the small *Zea* sp. pollen disappears (morphologically modern maize pollen remains), and domesticated sunflower (*Helianthus annuus*) appears. A sunflower seed and a sunflower fruit were AMS dated to 2667 calendar yr B.C. and 2548 calendar yr B.C., respectively (intercept dates) (Table 1). These are the earliest known examples of a fully domesticated sunflower (*11*). This discovery suggests that the theories pertaining to the origin of the domesticated sunflower in the eastern United States (*12*) now need revision. Cotton (*Gossypium* sp.) pollen also appears ca. 2500 calendar yr B.C. in the SAV2 core. Its appearance with other indicators of increased agricultural activity suggests domestication, although this interpretation cannot be confirmed from the pollen alone, and wild *Gossypium* sp. does occur in the Gulf Coast region farther to the east (*13*).

The earliest direct (AMS) dates on maize cobs in Mexico are ca. 4300 calendar yr B.C. (5400 yr B.P.) from highland Oaxaca (*14*). Analyses of these fully domesticated maize cobs and similar early cobs from highland Tehuacán confirm that domestication must have occurred before 4000 calendar yr B.C. (*10*). Our pollen evidence from Tabasco suggests that initial maize domestication occurred at least 1000 years earlier (i.e., before 5000 calendar yr B.C.). The occurrence of *Manihot* sp. at San Andrés indicates indirect contact with farmers in the Amazon basin, where DNA evidence suggests that manioc was domesticated (*15*). Such an early appearance of maize and manioc in lowland Tabasco adds support for the proposed origin of New World agriculture in a humid tropical setting, and for the early exchange of cultigens between Mesoamerica and lowland regions of Central and South America (*14*, *16*, *17*).

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Role of Rab9 GTPase in Facilitating Receptor Recruitment by TIP47

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Mannose 6-phosphate receptors (MPRs) deliver lysosomal hydrolases from the Golgi to endosomes and then return to the Golgi complex. TIP47 recognizes the cytoplasmic domains of MPRs and is required for endosome-to-Golgi transport. Here we show that TIP47 also bound directly to the Rab9 guanosine triphosphatase (GTPase) in its active, GTP-bound conformation. Moreover, Rab9 increased the affinity of TIP47 for its cargo. A functional Rab9 binding site was required for TIP47 stimulation of MPR transport in vivo. Thus, a cytosolic cargo selection device may be selectively recruited onto a specific organelle, and vesicle budding might be coupled to the presence of an active Rab GTPase.

Mannose 6-phosphate receptors (MPRs) deliver newly synthesized lysosomal hydrolases from the Golgi complex to prelysosomes and then return to the trans-Golgi network (TGN) to pick up more cargo (*1*, *2*). Export of MPRs from the Golgi is mediated by the AP-1 adaptor complex, which binds MPR cytoplasmic domains and recruits these receptors into clathrin-coated vesicles. MPR transport from endosomes to the Golgi is mediated by a protein named TIP47 (tail-interacting protein of 47 kD) that binds to a different signal in MPR cytoplasmic domains and is required for their recycling to the Golgi both in vitro and in vivo (*3*). Finally, MPR endocytosis is mediated by the AP-2 clathrin adaptor at the plasma membrane (*1*, *2*).

A fundamental question in cell biology is how a single receptor is recognized by different transport machineries depending on its intracellular location. One possibility is that

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