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4 ANTHROPOCENTRIC FOOD WEBS IN THE PRECOLUMBIAN AMERICAS

The greatest environmental impact brought about by ancient Americans revolved around their interaction with domesticated organisms, mostly plants, that were incorporated into highly interconnected trophic webs with humans as primary consumers. A trophic web is a set of populations whose interactions are intensely linked and act as a subunit of a larger community, with only loose connections to other subunits (Putnam 1994:40). The evolution of anthropocentric trophic webs had five profound effects on the Precolumbian landscape: (1) they greatly extended the range and enlarged populations of organisms within the human-centered trophic webs; (2) species, such as ruderals and vermin, that could adapt to environmental disturbances caused by the expansion of human settlements proliferated; (3) habitat for native species outside the webs was reduced; (4) plants and animals sought as prey species were affected, most commonly reduced in numbers; and (5) the efficient and flexible nature of cultivated organisms within the trophic webs allowed large-scale expansion of human populations into aggregated settlements in several different regions. Because of differences in available resources and variability in human groups, not all trophic webs throughout the Americas were the same. While some Native Americans remained totally dependent on wild foods until European contact, others incorporated domesticates into their food procurement strategies. Before attempting to discuss the overall impact of these developments, let us examine the effects of climate and how relationships, initially predator-prey interactions, between humans and other members of their trophic webs began.

CLIMATE

The climate in Central America at the end of the Pleistocene was cooler than it is today with less pronounced seasonality cycles (Byrne 1987). Modern or post-Pleistocene vegetation became established sometime between 11,000 and 6,000 years ago (Hunter et al. 1988; Pearsall 1995). However, there have been many prolonged wet periods and droughts since the end of the Pleistocene (see Hodell et al., this volume), and this caused a shifting in the ranges of most species, both north and south and up and down in elevation, since the beginning of the Holocene (Webb 1987).

As the Pleistocene drew to a close and the Pleistocene megafauna disappeared with it, perhaps as a result of human influences (Martin and Wright 1967; MacPhee and Marx 1997), an ameliorated climate and a different set of predator options faced the remaining and proliferating human populations at the outset of the Holocene. Gone were the large game animals that formed at least part of Paleoindian food intake, so there must have been some alteration of dietary habits. Fortunately for the early Holocene occupants, many of the plants adapted to the new climate were annuals, "*r* strategists" with a high intrinsic rate of increase (Jones 1997:158). This meant they would set seed at the end of a short growing season and produce copious numbers of seeds to insure reproductive success in an unpredictable environment. Geophytes, or plants with underground storage organs (e.g., tubers), also proliferated at the end of the Pleistocene and throughout the Holocene. They are the kind of plants that do well in a variable climate and thrive in disturbances caused by human occupation. Generally, reports of late Pleistocene–early Holocene sites do not include information about plant remains, but the ones that have been published tell us something of that early transition to a diversified hunting and gathering adaptation (table 4.1).

Archaeological sites from late Pleistocene–early Holocene times provide a set of randomly connected snapshots of the transition from hunting and gathering to early agriculture. What we can see from this filtered mosaic is a portent of subsequent patterning: exploitation of tree fruits began early and continued through the contact period, weedy annuals and geophytes were gathered (often from campsites and other areas of human disturbance), and some became the ancestors of domesticates. All the while, symbiotic microorganisms were developing vital interactions with many useful plants. One of the few large-seeded New World grasses, teosinte, was gathered as a wild food. Later, through a series of fortunate mutations, it was transformed into a diminutive form of maize, which was adopted and exploited by incipient mesoamerican horticulturalists. All told, the picture of the New World foragers that preceded agriculturalists is not a sharp one, but what does seem clear is that the transition was gradual, probably taking more than six or seven millennia. During that time, humans gained knowledge about useful organisms and developed much tighter connections with all components of their trophic webs.

TABLE 4.1. ARCHAEOLOGICAL EVIDENCE FOR EARLY PLANT USE

Site	*Date*	*Plant remains*	*Author*
Monte Verde, Chile	11,000 B.C.	wild potatoes (*Solanum* sp.)	Dillehay 1989 Ugent et al. 1987
Pedra Pintada, Brazil	9–8000 B.C.	palms (*Attalea* spp. and *Astrocaryum vulgare*), other trees (*Hymenaea* spp., *Sacoglottis guianensis, Bertholletia excelsa* and *Byrsonima crispa*)	Roosevelt et al. 1996
La Yeguada, Panama	9–8000 B.C.	burnt tree species	Piperno et al. 1990, 1991a, b
Hester, U.S.	9–6000 B.C.	hickory (*Carya* spp.), acorns (*Quercus* spp.), black walnuts (*Juglans nigra*), hackberry (*Celtis* sp.), and wild plums (*Prunus americana*)	Lentz 1986
Gainesville, U.S.	8500–8000 B.C.	acorns, hickory nuts, persimmon (*Diospyros virginiana*)	B. D. Smith 1986
Rodgers Shelter, U.S.	8500–8000 B.C.	hickory nut, black walnut, hackberry (*Celtis occidentalis*)	Wood and MacMillan 1976
San Isidro, Colombia	8000 B.C.	palms (*Acrocomia aculeata*), wild avocados (*Persea* sp.) and roots	Gnecco Valencia 1994 Piperno and Holst 1997
Peña Roja, Colombia	7200 B.C.	palm (*Oenocarpus* sp.)	Cavelier et al. 1995
Guilá Naquitz, Mexico	8–6000 B.C.	acorns, hackberry, mesquite (*Prosopis juliflora*), *Dalea,* prickly pear (*Opuntia* sp.), squash (*Cucurbita pepo*) in early levels. Bottle gourds (*Lagenaria* sp.), avocados (*Persea americana*), and common beans (*Phaseolus vulgaris*) in more recent levels	Flannery 1986 C. E. Smith 1986 B. D. Smith 1997a Whitaker and Cutler 1986
Zohapilco, Mexico	6000–2200 B.C.	goosefoot (*Chenopodium* sp.), *Amaranthus* sp., tomatillo (*Physalis* sp.), and teosinte (*Zea mays* ssp. *mexicana*)	Niederberger 1979
Koster, U.S.	5000–2900 B.C.	squash, marshelder (*Iva annua*), hickory, acorns, black walnuts, pecan (*Carya illinoensis*), goosefoot (*Chenopodium* spp.), grape (*Vitis* sp.), smartweed (*Polygonum* spp.), wild bean (*Strophostyles* sp.), hackberry, wild plum, pokeweed (*Phytolacca americana*), hawthorn (*Crataegus* sp.), green briar (*Smilax* sp.), *Viburnum* sp., Solomon's seal (*Polygonatum* sp.)	Conard et al. 1984 Asch et al. 1972
Ocampo Caves, Mexico	4500–1100 B.C.	bottle gourd, squash (*Cucurbita pepo*), avocado, acorns, common beans, runner beans, foxtail grass, peppers, sunflower (*Helianthus annuus*), amaranth, and maize	B. D. Smith 1997a MacNeish 1992
Tehuacán Valley, Mexico	3500 B.C.–A.D. 1500	foxtail grass (*Setaria* cf. *macrostachya*), peppers (*Capsicum annuum*), amaranthus, mesquite, avocado, ciruela (*Spondias mombin*), prickly pear, peanuts (*Arachis hypogaea*), jack beans (*Canavalia* sp.), runner beans (*Phaseolus coccineus*), sieva beans (*P. lunatus*), common beans, guava (*Psidium guajava*), cotton (*Gossypium hirsutum*), squash (*Cucurbita pepo, C. mixta, C. moschata*), and maize (*Zea mays*)	C. E. Smith 1967 Long et al. 1989

TROPHIC WEBS IN THE AMERICAS

As with most aspects of nature, humans are parts of networks of groups of organisms that are intertwined through multiple facets of their life cycles. Most of these networks, or trophic webs, have anthropogenic orientations as a result of several thousand years of both conscious and unconscious human manipulation. Humans have organized the funneling of major portions of the food web output for themselves. This is similar to what some authors have referred to as "agroecology," yet is more comprehensive in scope. Rindos (1984 : 122) defines agroecology as a system that includes humans, their domesticates, and associated ruderals. Defining the interaction in this way reflects Western cultural bias; humans grow food (keep out the weeds), eat it, and then get rid of the waste. Or in a more urban context, humans go to the supermarket, buy food (herbicides have already taken care of the weeds), consume it, throw out the trash, and flush the waste. This is not a cycle, but a unidirectional flow from autotrophs to heterotrophs. The cycle of a trophic web is more intricate because it includes large groups of other organisms that are closely and essentially involved with agroecological systems in addition to the autotrophs and heterotrophs that are generally the sole topics of discussion.

Figure 4.1 outlines some of the key elements in human-centered trophic webs. At the center are humans and their domesticated animals feeding off domesticated plants (autotrophs) as the core interaction of the agroecological system. Their remains and waste products are consumed by scavengers and detritivores (mostly bacteria, fungi, and protistans). These organisms are largely responsible for the breakdown and fragmentation of macromolecules (carbohydrates, proteins, fats, etc.) that ultimately release minerals and other nutrients into the soil. Lacking the dung of large domesticated animals (although the Andean peoples with their camelids were exceptions), many Native American groups were careful to recycle human waste. For example, the Aztecs at the time of the Conquest were observed saving their excrement for later use (Díaz 1963 : 233). Today, the Yucatec Maya intentionally defecate in their dooryard gardens (Hanks 1990 : 335) to fertilize them. Even though they were probably unaware of the details, Native Americans were aiding the cyclical flow of nutrients within their trophic webs.

Also in figure 4.1 are wild plants and animals that were always part of the Precolumbian resource base. Note that in close association with the autotrophs are mycorrhizal fungi and bacteria that have coevolved with their host plants. These organisms are essential components of the trophic web in all regions of Precolumbian America (and all other agricultural systems, for that matter). They live in close proximity and form a symbiotic relationship with the root systems of many of the most important crops, promoting the absorption of minerals and in some cases even manufacturing vital nutrients.

The *Rhizobium* spp., *Azorhizobium* spp., and *Bradyrhizobium* spp. symbionts (Giller and Wilson 1991 : 32) of beans and other legumes are well known for their ability to convert gaseous nitrogen into solid nitrates that can be absorbed by the host

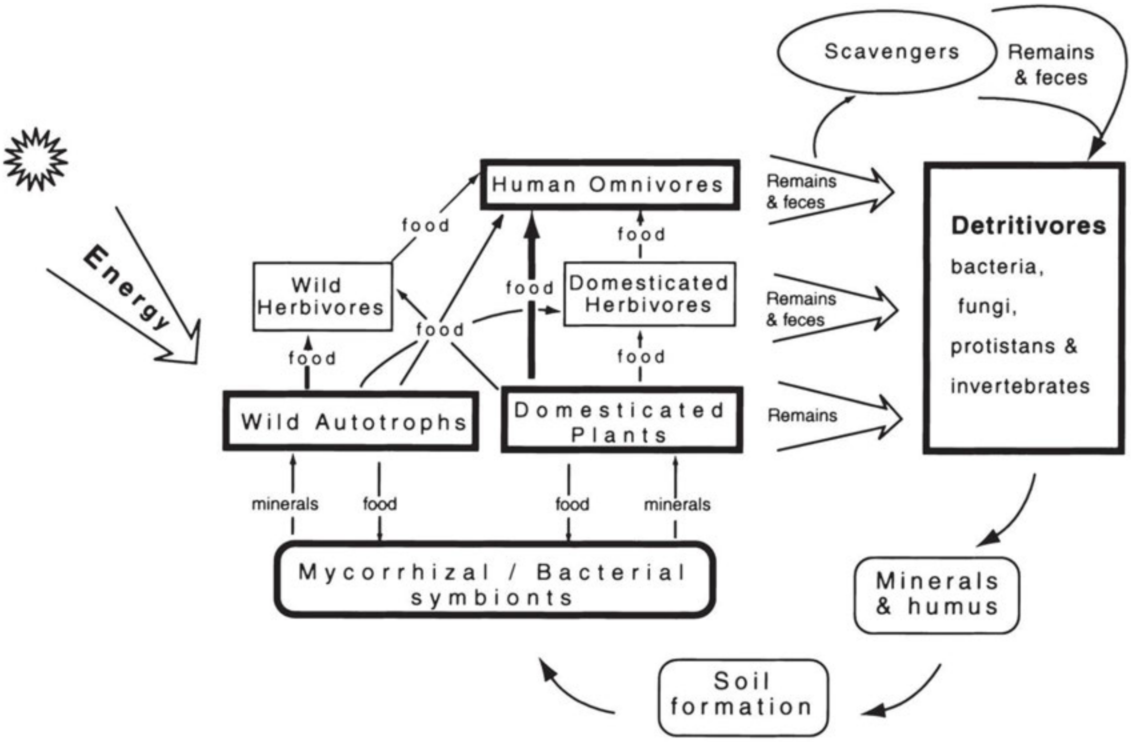

FIGURE 4.1. A human-centered trophic web.

plant (Harley and Smith 1983:369). Nitrogen-fixing bacteria have two dramatically important effects on the heterotrophic components of the web: they help to enrich the surrounding soil with nitrogen compounds, and they make nitrogen available to the leguminous host plants (which in turn convert it to compounds rich in nitrogen, e.g., amino acids and proteins). When consumed, legumes are highly nutritious dietary components and undoubtedly helped to sustain many bean-eating Precolumbians when no meat was available. As a component of the agricultural system, the nitrogen-fixing bacteria in leguminous root nodules helped to restore soils impoverished by crops that absorb nitrates but have no direct mechanism to return what they have consumed.

Mycorrhizal fungi work in a different way; they do not manufacture usable minerals, but through their extended hyphae and close proximity to living root tissues they greatly enhance the host plant's ability to absorb minerals that are in the soil, especially phosphorus (Harley and Smith 1983:38). Many domesticates form mycorrhizal associations (e.g., maize, tobacco, beans, potatoes, manioc, cacao, tomatoes, avocados, and cotton) and have stunted growth in the absence of appropriate symbionts (S. E. Smith and Read 1997). Modern reforestation efforts, plantation projects, and agricultural plantings are often accompanied by fungal inoculations to insure proper mycorrhizal development (Harley and Smith 1983:404). Even though mycorrhizal species are less host specific than nitrogen-fixing bacteria, and a range of mycorrhiza may infect host plants, there is a marked difference in symbiotic effectiveness (ibid.:378). In short, most crops that form symbiotic relationships with ground-dwelling microorganisms need the right symbionts to grow and mature effectively.

Understanding the agroecology of trophic webs is critical for understanding the origins of agriculture. As suggested above, there is much more to agricultural systems than just humans and domesticates. Wild plants, for example, did not simply fall out of use as food, even after the adoption of agriculture, but remained important resource components of all webs. In addition to asking how, where, why, and by whom plants became domesticated, it is important to consider how wild plants adapted to the human-centered trophic webs. How are humans, domesticates, and wild plants interconnected? What input did domesticated verses nondomesticated plants have on food webs? Did wild plants continue to serve as a genetic reserve through introgression and hybridization? As plant tending turned from a singular process, gathering, to a complex process, agriculture, how did this affect the question of who was involved with what aspects of plant tending? All of these questions address important aspects of human-centered trophic webs and their associated organisms, yet none can be easily answered.

Equally important as organisms that can be seen with the unaided eye are ones that cannot. Root symbionts might have had two effects on early agriculture: (1) they enhanced its productivity, and (2) they may well have influenced its rate of expansion, especially in terms of trade from one region to another. Many Native American groups, such as the Maya (Vogt 1993:56), traditionally intercropped their fields with maize and beans. Studies have shown that maize, beans, and squash grown in polyculture produce higher yields than monoculture stands of the same crops (Tuxill and Nabhan 1998). The nitrogen-fixing bacteria in the root nodules of beans improve usable nitrogen content of the soil, and mycorrhizal fungi in the roots of maize and beans enhance their ability to absorb phosphorus. Conversely, if a crop was transported to a region without its symbionts, as might have occurred when seeds were exchanged through long-distance trade, its productivity in the new region would have been reduced. This lowered productivity may have acted as a disincentive for the crop's adoption for general use. Perhaps this is why maize was not popular for a long time after its first introduction into eastern North America; possibly its symbionts were not available, and the newly introduced crop did not do well without them. In the case of down-the-line trade of cultigens to neighboring lands, it is more likely that the right symbionts would be in the area of introduction. Also, the shorter time span involved might have made it more likely that the spores of symbionts would be transported along with the seeds, thus insuring that the correct symbionts would be present in the new area.

INTEGRATING DATA AND THEORY: THE MESOAMERICAN EXAMPLE

Archaeological and paleoenvironmental studies are beginning to reveal some of the conditions that existed in the early Archaic that may have precipitated the incorporation of domesticates into the New World trophic webs. These include the availability of domesticable species with coevolved symbionts, technocultural preadaptations for agriculture, e.g., storage and food processing capability, and a climatic regime characterized by strong seasonality. As described above, many different wild plants were exploited for their high yield of nutrients and, in some cases, were processed using a variety of specialty tools (e.g., grinding and chopping stones). Surpluses may have been stored for later consumption in storage pits and through other kinds of storage technology. These are common features found at the earliest Tehuacán Valley sites (Byers 1967), Guilá Naquitz (Flannery 1986), and Tamaulipas (MacNeish 1958). The ability to store surplus food was an important step in the growing hegemony of the energy flow in trophic webs as it gave humans the ability to monopolize available nutrients and exclude competing organisms. Also, the innovation of storage facilities with sequestered food supplies created a buffer against the vagaries of an unpredictable yet periodically bountiful environment. Ford (1968) observed that the reduction of risk from periodic drought was a strong motivating factor in community planning among the Tewa in the North American Southwest. This reduced risk may have been accompanied by concomitant reduced mobility because quantities of stored food and grinding stones are not readily portable. Archaic hunters and gatherers need not have been completely sedentary, i.e., inhabiting one location throughout the year, to make the investment in storage facilities and heavy grinding stones worthwhile. The preponderance of archaeological data from the Tehuacán and Oaxaca valleys indicate the occupants were seasonally transhumant. Nevertheless, the presence of storage units clearly implies the intent to occupy sites for extended periods or at least to reoccupy them.

Increased sedentism most likely affected the population structure by increasing fecundity and reducing infant and child mortality. Kelly notes (1995:259) that in hunting and gathering groups, a highly variable diet as a result of seasonality as well as frequent aerobic activity and prolonged breastfeeding results in lowered fecundity. Also, infant and child mortality is high in hunting and gathering groups because mobility exposes children to higher risks of accidents, disease, and parasites. As such, mobility and group size are inversely correlated through a complex array of social, biological, and psychological mechanisms. All of these factors combine so that once storage and specialty tool innovations have been adopted, they increase the cost of residential mobility, making it more difficult to abandon whatever food production and storage capabilities have been developed. Neo-Darwinists (Bettinger 1991) might comment that these adaptations would lead to increased fitness, so the reproductive units adopting sedentary and stable food-obtaining mechanisms would have an advantage over competing groups without the adaptations. In this way, hunters and gatherers can become enmeshed in what systems theorists (e.g., Bertalanffy 1962; Miller 1965) refer to as deviation amplifying behavior. Postprocessualists (Hodder 1995) would argue that these innovations led to economic and cultural attachments to particular places. Indeed, neither perspective need be opposed; storage and sedentism certainly involved a host of physical, economic, and cultural changes, all of which were interrelated in varying ways for different groups of peoples.

The food storage habits of Archaic Americans probably helped them endure the uncertain nature of the climatic pattern, and these innovations may have been coupled with other options for coping with uncertainty. One option was to develop techniques that would enhance the productivity of desirable plants. This could have been done in many ways, short of a headlong plunge into agriculture. Steward (1934) observed Paiutes in Nevada, essentially hunters and gatherers, irrigating open fields supporting wild sunflowers (*Helianthus bolanderi*), goosefoot (*Chenopodium* spp.), sage (*Salvia columbariae*), wild rice (*Oryzopsis hymenoides*), and *Eleocharis* sp. that had not been planted or even cultivated. (Cultivation here means to turn the soil to promote growth of a specific plant, whether wild or domesticated.) Other groups, e.g., Native Californians, burned areas to promote growth of certain weedy species that would gain a competitive advantage over less useful plants following a fire (Bean and Lawton 1976: 30). Many ethnographic instances of the broadcasting of wild seeds have been recorded (Harlan 1975:23). This enhancement of desirable wild plants would have been another predomestication mechanism to expand the food supply. When coupled with burning, dissemination of wild seeds would have been an effective way of enhancing growth of useful food plants. Plants, especially ones with a plastic nature like weedy annuals, would soon have responded to this kind of activity so that characteristics (such as uniform seed set, larger seed size, tough rachises, etc.) more compatible with human activities would evolve rapidly and quite possibly without the knowing intervention of human manipulators.

Directed change began to occur when humans started disseminating plant propagules and, ultimately, selected plants with desired phenotypes, just as is practiced among the Tzotzil Maya, who set aside the largest and best ears of maize from each harvest for future planting (Vogt 1993:55). Accordingly, human decision-making would have played a huge role in this process, not only in terms of developing and selecting improved cultivars but also in terms of adopting previously developed cultigens from other areas. Some of the New World crops may have been domesticated only once and then disseminated from a single source. This is an example of the way human agency played a pivotal role: creativity was an essential component of the domestication process. Crop development would have led to improved productivity, would impact a sedentary group's ability to sustain larger numbers, and, ultimately, led to inclusion of domesticated plants and animals in the human-centered trophic web.

Even as Precolumbian American societies became more dependent on agriculture, they continued to exploit wild plants (mostly ruderals) and especially wild animals. For example, the Maya, among the most dependent on agriculture of New World peoples, relied upon wild plants as a component of their diet throughout the prehistoric period (Vogt 1993:51; Lentz 1991). Yucatec Maya commonly plant a field for two or three years then allow it to fallow for five to fifteen years (Hanks 1990:358–361). While land is left in fallow, it is not useless; weedy herbaceous species, pioneer shrubs, and trees move in and become established, making excellent sites for gathering wild foods and medicinal plants and hunting game that would come to forage on the verdant growth in a fallowed field. Many pioneer species are legumes (e.g., *Acacia* spp., *Gliricidia sepium,* and *Inga* spp.), and these have *Rhizobium* spp. symbionts in their root nodules, thus improving the nitrate content of the soil. Nitrogen fixation undoubtedly is a significant factor in the rejuvenation of fallow fields. Most pioneer species have mycorrhizal symbionts that help to incorporate minerals into the biomass of the fields, which, after burning, is available for use by crop plants. This pattern probably was repeated in various agricultural regions of the New World, often with different species involved, forming unique webs in different environmental settings.

MAJOR NEW WORLD DOMESTICATES

The best estimates indicate that the domestication process began in the New World at least by 8000 B.C. The development of crops did not happen in the same place at the same time. It is possible that domestication was an idea that developed in certain areas first and diffused into other areas, thus encouraging neighboring groups to experiment with local plants of apparent utility. Table 4.2 outlines a list of plants domesticated in the Americas and their probable wild ancestors. The approximate distribution of New World domesticates at the time of European contact and the natural distribution of their wild progenitors also is included in the table. Following is a discussion of a few of the more important American crops, all derived from weedy annuals or geophytes, beginning with the first domesticated.

SQUASHES

In what may have been the earliest New World domesticate, *Cucurbita pepo* appears to have been under domestication in the Oaxaca Valley at least by 8000 B.C. (B. Smith 1997a,b). Probably the plant was grown initially for its seeds rather than its flesh, which, in wild cucurbits, is quite bitter (Whitaker and Bemis 1975). *C. fraterna,* a wild gourd of northeastern Mexico, has been proposed as the wild progenitor of *C. pepo* (Nee 1990), but molecular studies have questioned this relationship (Decker-Walters et al. 1993). Other early domesticated Cucurbitaceae from archaeological contexts include *Lagenaria siceraria* (gourd) (4490 B.C.) and *C. argyrosperma* (3085 B.C.) from the Tamaulipas caves (B. Smith 1997a,b).

BEANS

Beans, both common and lima, were important components of the trophic web in most parts of the Precolumbian Americas where agriculture was practiced. Data generated by electrophoretic analysis of a seed storage protein, phaseolin, suggest beans may have originated in both Mesoamerica and South America. Apparently, the "S" phaseolin protein, common in most bean cultivars, seems to have originated in Mesoamerica, while "B," "A," "C," "H," and "T" phaseolin types have South American origins (Gepts 1990). The chronology of early bean remains from several archaeological sites has been reevaluated using accelerator mass spectrometry (AMS) technology (Kaplan and Lynch 1999) and the results give us fresh insights. The earliest common bean from the Andean Highlands at Guitarrero Cave, a site excavated in the 1970s (Lynch 1980), was dated at 4337±55 B.P. The earliest bean remains, pods from Chilca Cave on the

TABLE 4.2. CROPS OF THE AMERICAS, THEIR WILD PROGENITORS, AND DISTRIBUTION AT TIME OF CONTACT

Domesticated Plants	*Distribution at Contact*	*Wild Progenitors*	*Wild Distribution*	*Reference*
Dicots				
Amaranthaceae				
Amaranthus cruentus L. amaranth	Mexico, Central America, tropical South America	*A. powellii* S. Wats?	Mexico, eastern and western United States	Towle 1961, Harlan 1995, Cole 1979, Pickersgill and Heiser 1977
A. caudatus L. amaranth	Andes: Peru–northwest Argentina	*A. quitensis* HBK.?	north Argentina, south-central Andes	Harlan 1995, Cole 1979
A. hypochondriacus L. amaranth	Mexico, southwest and eastern United States, Central America	*A. hybridus* L.?	temperate and tropical New World (Mexico?)	Harlan 1995, Cole 1979, Pickersgill and Heiser 1977
Anacardiaceae				
Anacardium occidentale L. cashew	Central America, lowland South America	wild *A. occidentale*	south Brazil	Mitchell and Mori 1987
Spondias purpurea L. jocote	Mexico, Central America, West Indies, North and South America	wild *S. purpurea*	Mexico, Central America	Williams 1981
Annonaceae				
Annona cherimola Mill. cherimoya	Peru	wild *A. cherimola*	Andean valleys of Peru, Ecuador	Purseglove 1974
A. muricata L. guanabana	Central America to coastal Peru	*A. montana* Macfad.	Costa Rica to northern South America, West Indies	Safford 1914, Purseglove 1974, Schatz 1987
Apiaceae				
Arracacia xanthorrhiza Bancr. arracacha	Andean Bolivia to Venezuela	?	Andean Peru? Bolivia?	Hermann 1992, Purseglove 1974
Asteraceae				
Helianthus annuus L. sunflower	southwest to eastern United States, Mexico, Central America	*H. annuus* ssp. *lenticalaris* (Dougl.) C. Kll. *H. annuus* ssp. *jaegeri* Heiser *H. annuus* ssp. *annuus* L.	western United States, Mexico	Heiser 1985, Rieseberg and Seiler 1990
Iva annua L. marshelder	southwestern and central United States	wild *I. annua*	central United States	Smith 1995, Gleason and Cronquist 1991
Basellaceae				
Ullucus tuberosus Calda. ssp. *tuberosus* Sperling ulluco	Andean Argentina to Venezuela	*U. tuberosus* ssp. *aborigineus* Sperling	Andean Peru to Argentina	King 1998
Bignoniaceae				
Crescentia cujete L. calabash	Mexico to northern South America	wild *C. cujete*	Mexico, Central America	Williams 1981

Bixaceae				
Bixa orellana L. achiote	Mexico to Amazonia	*B. excelsa* Gleason & Krukoff	southwestern Amazon	Schultes 1984
Brassicaceae				
Lepidium meyenii Walp. maca	central Peruvian Highlands	wild *L. meyenii*	Peru, Bolivia, Argentina	King 1988
Cactaceae				
Opuntia spp. prickly pear	Mexico, southwestern United States, Central America	wild *Opuntia* spp.	Mexico, southwestern United States	Williams 1981, Ebeling 1986
Caricaceae				
Carica papaya L. papaya	Central America to Amazonia, coastal Ecuador	*C. microcarpa* Jacq. *C. pubescens* Lenne & Koch. *C. goudotiana* (Tr. & Planch.) Solms	northwestern South America	Prance 1984
Chenopodiaceae				
Chenopodium berlandieri ssp. *nuttaliae* (Safford) H. D. Wilson & C. B. Heiser goosefoot	central Mexico, central United States	*C. berlandieri* ssp. *berlandieri* Moq.	eastern and western United States to Mexico	Wilson 1990
C. quinoa Willd. quinoa	Andes, Colombia to northern Chile, northern Argentina	*C. hircinum* Schrad?	northern Argentina, Uruguay, southern Brazil	Wilson 1990
Convolvulaceae				
Ipomoea batatas (L.) Lam. sweet potato	lowland Neotropics	*I. trifida* (HBK.) G. Don.	Central America, northern South America ??	Austin 1978, Piperno and Pearsall 1998, Purseglove 1974
Cucurbitaceae				
Cucurbita argyrosperma Huber squash	southwestern United States to Guatemala	*C. sororia* Bailey	Pacific coast of Mexico to Nicaragua	Nee 1990
C. ficifolia Bouché squash	Andean South America, Mexico	?	Bolivia?	Nee 1990
C. maxima Duch. squash	western slopes of the Andes	*C. andreana* Naud	Uruguay and northern Argentina	Nee 1990
C. moschata (Lam.) Poir butternut	southwestern United States to northern South America	?	southern Central America? to Colombia?	Piperno and Pearsall 1998: 199, Nee 1990
C. pepo L. squash, pumpkin	eastern United States, southwestern United States, Mexico	*C. fraterna* Bailey	northeastern Mexico to southeastern United States?	Nee 1990
Lagenaria siceraria bottle gourd	North America, South America, Central America, Mexico, West Indies	?	southeastern Africa	J. D. Sauer 1993, Purseglove 1974
Sechium edule (Jacq.) Sw. chayote	Mexico, Guatemala, Honduras	*S. compositum* (Donn. Sm.) C. Jeffrey	Mexico, Guatemala	Newstrom 1991, Lentz 1991

(*continued*)

TABLE 4.2. *(Continued)*

Domesticated Plants	*Distribution at Contact*	*Wild Progenitors*	*Wild Distribution*	*Reference*
Erythroxylaceae				
Erythroxylum coca Lam. var. *ipadu* T. Plowman coca	Andean Ecuador to northern Argentina	*E. coca* Lam.	eastern Peru	Plowman 1984
E. novogranatense (Morris) Hieron. coca	coastal Peru to Costa Rica?	*E. coca* Lam.	eastern Peru	Plowman 1984, Schultes 1984
Euphorbiaceae				
Manihot esculenta Crantz. manioc	Central America, Mexico, Amazon Basin, Pacific coast South America	*M. esculenta* ssp. *flabellifolia* *M. tristis* Muell-Arg. *M. irwinii* Rogers	Guianas or Central Brazil	C. O. Sauer 1952, Stone 1984, Fregene et al. 1994
Lauraceae				
Persea americana Mill. avocado	Mexico to Peru	wild *P. americana*	Guatemala to central Mexico	B. D. Smith 1992, Schieber and Zentmeyer 1978
Leguminosae				
Arachis hypogaea L. peanut	South America lowlands, West Indies, midelevation Andes	*A. monticola* Krop. & Rio	northwestern Argentina	Stalker 1990, J. D. Sauer 1993, Piperno and Pearsall 1998
Canavalia ensiformis (L.) DC sword bean	Mexico, West Indies, Central America, coastal Peru and Ecuador	*C. brasiliensis* (Benth.) Mart.	Central America and West Indies	Purseglove 1974, Kaplan and Kaplan 1988
C. plagiosperma Piper. jack bean	coastal Ecuador and Peru	*C. piperi* Killip & Macbride	central Brazil, northeastern Bolivia, northwestern Argentina	Purseglove 1974, Piperno and Pearsall 1998, J. D. Sauer 1964
Indigofera suffruticosa Mill. añil	Mexico to South America, West Indies	wild *I. suffruticosa*?	Mexico, Central America	Dering 1895, Williams 1981
Pachyrrhizus erosus (L.) Urban jicama	Mexico, tropical South America, Central America			Harlan 1995
Phaseolus acutifolius A. Gray tepary bean	southwestern United States, Mexico, Central America to northern Nicaragua	*P. acutifolius* var. *acutifolius* (Wild.)	northwestern Mexico, southwestern United States	Pratt and Nabhan 1988
P. coccineus L. scarlet runner bean	Mexico	*P. coccineus* ssp. *formosus* (Kunth.) Maré., Masch. & Stain.	Mexico, Guatemala	Delgado et al. 1988
P. lunatus L. lima bean	Mexico to Andes and west coast South America	*P. lunatus* var. *silvester* Baudet	southern Mexico to central Argentina below 1,000 m	Baudoin 1988, Kaplan and Kaplan 1988

P. vulgaris L. common bean	Andes (Chile–Ecuador), Central America, Mexico, southwest and eastern United States	*P. vulgaris* var. *mexicanus* A. Delgado *P. aborigineus* Burk.	west-central Mexico to southern Andes	Gepts 1990, Kaplan and Kaplan 1988, Delgado et al. 1988, Brücher 1968
Malphigiaceae				
Byrsonima crassifolia (L.) DC nance	Mexico to northern South America	wild *B. crassifolia*	Mexico (to northern South America?)	Williams 1981
Malvaceae				
Gossypium barbadense L. cotton	Central America, West Indies, Andes, western South America, Amazonia	wild *G. barbadense*?	western South America	Percy and Wendell 1990, Purseglove 1974, Fryxell 1979
G. hirsutum L. cotton	Mexico, southwestern United States (?), Central America, West Indies, northeastern Brazil	wild *G. hirsutum* *G. thurberi* Tod.	Central America and South America	Purseglove 1974
Moraceae				
Brosimum alicastrum Swartz. breadnut, ramón	Mexico, Central America	wild *B. alicastrum*	Mexico	Purseglove 1974
Myrtaceae				
Psidium guajava L. guava	Mexico to Peru, West Indies	wild *P. guajava*	Panama, Neotropical	Popenoe 1948, Purseglove 1974
Oxalidaceae				
Oxalis tuberosa Mol. oca	Andean Chile to Venezuela	?	Andes above 2,500 m	King 1988
Rosaceae				
Prunus capuli Cav. Mexican cherry	Mexico, Central America	wild *P. capuli*	Mexico, western Guatemala?	Standley and Steyermark 1946
Sapotaceae				
Lucuma mammosa Gaertn. f. zapote	Mexico, Central America, West Indies, tropical South America	wild *L. mammosa*	southern Mexico to northern Nicaragua	Morton 1987
L. obovata Kuntze caimito	South America, West Indies	wild *L. obovata*	Colombia to Chile	Piperno and Pearsall 1998; Stanley and Steyermark 1946
Manilkara zapota (L.) van Royen sapodilla	Mexico, Central America, West Indies, lowland tropical South America	wild *M. zapota*?	southern Mexico, Central America	Morton 1987
Solanaceae				
Capsicum annuum L. chile, bell pepper	southern Mexico to Colombia, West Indies	*C. annuum* var. *glabrisculum* (Dun.) Heiser & Pickersgill	southern United States to northern South America	Andrews 1995, Pickersgill 1971, Eshbaugh et al. 1983, Heiser 1976

(*continued*)

TABLE 4.2. (*Continued*)

Domesticated Plants	*Distribution at Contact*	*Wild Progenitors*	*Wild Distribution*	*Reference*
C. *baccatum* L. ají pepper	southern Amazon to Argentina, South America Pacific coast	C. *praetermissum* Heiser & Smith	southern Brazil	Andrews 1995, Eshbaugh et al. 1983, McLeod et al. 1982, Pickersgill 1984
C. *chinense* Jacq. habañero pepper	Amazonia, West Indies, Central America, coast of South America: Ecuador to Chile	C. *chacoense* var. *tomentosum* A. T. Hunziker	Bolivia	McLeod et al. 1982, Andrews 1995, Eshbaugh et al. 1983
C. *frutescens* L. tabasco pepper	West Indies, Central America, Amazon, Pacific coast Ecuador to Chile	wild C. *frutescens*	western Amazon of Colombia and Peru	Andrews 1995, McLeod et al. 1982
C. *pubescens* Ruiz & Pav. rocoto pepper	midelevation (2,000–2,500 m) Andes	C. *cardenassii* Heiser & Smith	Bolivia, upper Amazon	Andrews 1995, Eshbaugh et al. 1983
Lycopersicon esculentum Mill. tomato	Mexico to South America	*L. esculentum* var. *cerasiflora* (Dun.) A. Gray	northwestern Peru (foothills of Andes)	Rick and Holle 1990
Nicotiana tabacum L. tobacco	eastern South America, Colombia, Central America, Mexico, West Indies	*N. sylvestris* Spregazzini & Comes *N. tomentosiformis*	northwestern Argentina, Bolivia	Heiser 1992, Goodspeed 1954, Pickersgill 1977
N. rustica L. tobacco	western–eastern United States, Mexico, eastern Canada, South America	*N. rustica* var. *pavoni* (Dunal) Goodsp.?	Andean South America	Goodspeed 1954, Hill 1952, Purseglove 1974
Solanum tuberosum L. potato	pan Andean	*S. brevicaule* Bitter	Andean Peru, Bolivia	Grun 1990, Van den Berg et al. 1998
Sterculiaceae				
Theobroma cacao L. cacao, chocolate	southern Mexico to coast of Ecuador, Amazonia	*T. cacao* ssp. *sphaerocarpum* (A. Chevalier) Schultes	upper Amazon, northeastern South America	Young 1994, Schultes 1984
Tropaeolaceae				
Tropaeolum tuberosum R. & P. mashua	Andean Argentina to Venezuela	*T. tuberosum* ssp. *silvestre* Sparre	Colombia to Argentina above 2,400 m	King 1988
Monocots				
Agavaceae				
Agave fourcroydes Lem. henequin	Mexico, Central America	wild *A. fourcroydes*	Mexico	Purseglove 1972
A. sisalana Perr. sisal	Mexico, Central America	wild *A. sisalana*	Mexico, Central America	Purseglove 1972
Araceae				
Xanthosoma sagittifolium (L.) Schott malanga	Central America, tropical South America, West Indies	?	Central America	Purseglove 1972, Ghosh et al. 1988

Arecaceae				
Acrocomia aculeata (Jacq.) Lodd. ex Mart. coyol	Mexico to Colombia, Amazon	wild *A. aculeata*	Central America	Lentz 1990, Henderson et al. 1995
Attalea cohune Mart. cohune	Mexico to Colombia low elevations	*A. cohune*?	Mexico to Nicaragua	Henderson et al. 1995
A. speciosa Mart. ex Spreng. babassu	Panama to Bolivia below 1000 m, Brazil	*A. speciosa*?	southern Central America to northern South America	Henderson and Balick 1991, Henderson et al. 1995, Piperno and Pearsall 1998
Bactris gasipaes HBK. pejibaye palm	coastal Ecuador to Central America, Amazonia	*B. microcarpa* Huber	western Amazon	Prance 1984, Clement 1986
Chamaedorea tepejilote Liebm. pacaya	Mexico to Colombia	wild *C. tepejilote*?	Mexico to Colombia	Henderson et al. 1995, Williams 1981
Elaeis oleifera (Kunth) Cortés corozo	Honduras to Colombia, Amazon	*E. oleifera*?	Honduras to northern Colombia	Henderson et al. 1995, Balée 1989
Bromeliaceae				
Ananas comosus (L.) Merrill pineapple	central Mexico to Amazon, coastal Ecuador and Peru	*A. microstachys* Lindman	western Amazonia	Schultes 1984, Ducke 1946
Cannaceae				
Canna edulis Kerr. achira	Neotropics, subtropics	?	northern Andes	Gade 1966, C. O. Sauer 1952, Piperno and Pearsall 1998
Dioscoreaceae				
Dioscorea trifida L. yam	Central America, northern South America, West Indies	?	northern South America	Piperno and Pearsall 1998, Coursey 1967, Purseglove 1972
Marantaceae				
Calathea allouia Lindl. leren	Central America, northern South America, West Indies	?	Brazil, Venezuela and/or Guianas	Piperno and Pearsall 1998, Purseglove 1972
Maranta arundinacea L. arrow root	West Indies, Central America and South America	?	West Indies, northern South America, Central America?	Piperno and Pearsall 1998, Purseglove 1972, Sturdevant 1969
Orchidaceae				
Vanilla planifolia Andrews vanilla	Mexico, Central America	wild *V. planifolia*	Mexico, Central America, West Indies, northern South America	Dering 1895, Rain 1996, Masefield et al. 1969
Poaceae				
Setaria macrostachya HBK. foxtail millet	Mexico, West Indies, southwestern United States	wild *S. macrostachya*	Mexico, southwestern United States	Rominger 1962, Ebeling 1986
Zea mays L. maize	southwest to eastern United States, Mexico, Central America, South America	*Z. mays* ssp. *parviglumis* Iltis and Doebley	Río Balsas Valley, Mexico	Doebley 1990

Pacific coast of Peru, were dated to 5616±57 B.P. (Kaplan and Lynch 1999). A tepary bean (*Phaseolus acutifolius*) and a common bean pod from the Tehuacán Valley date to approximately 2300 B.P. Based on these dates, the oldest archaeological bean remains from South America are far older than the earliest material from Mesoamerica. At face value, these archaeological data suggest that the first beans were domesticated in South America and then introduced to Mesoamerica sometime prior to 2,500 years ago. However, many questions remain unanswered about the distribution of phaseolins in wild Central and South American *Phaseolus* populations. Clearly, much more work needs to be done in the bean paleoethnobotanical arena.

As mentioned above, beans are key dietary and ecological components of most human-centered trophic webs. Enhancing their vegetative success, common beans form symbiotic relationships with *Rhizobium leguminosarum* and several species of vesicular-arbuscular mycorrhizae in the genus *Glomus* (Harley and Smith 1983:38). Without the input of legumes and their symbionts, American agroecological systems would have been far less productive.

MAIZE

Zea mays was the staple crop for most agricultural Precolumbian Americans from North America to temperate areas of South America. Studies based on cytological and molecular data reveal that maize was derived from wild populations of *Zea mays* ssp. *parviglumis* in south-central and western Mexico (Doebley et al. 1987, 1984; Iltis and Doebley 1984; Dorweiler et al. 1993). A central question is how this seemingly dissimilar, albeit large-seeded, wild grass evolved into the crop that became the mainstay of many New World agriculturalists. A complete answer to this question is still lacking, partly because we have so little paleoethnobotanical evidence relating to teosinte as a wild food or maize as an early cultigen. Evidence from the Zohapilco and Tehuacán Valley sites offers a few pieces to a puzzle that remains largely a blank slate. At Zohapilco, remains of amaranth, tomatillo, and teosinte were recovered from a setting suggesting that hunters and gatherers were collecting wild plant foods (Niederberger 1979). The inhabitants of the site were experimenting with at least two plants, amaranth and teosinte, that later developed into important domesticates.

Let us focus on teosinte for a moment; it was marginally useful but desirable as a wild food mostly because it has larger seeds than most other New World grasses. Each seed is contained within a hard fruitcase attached to a fragile spikelet, which releases the ripened fruitcase readily. The seed can be removed from the fruitcase by toasting and grinding or popping. It is a good bit of work for a small reward, but Archaic Mexicans found it worthwhile, probably as a minor dietary component. Tehuacán Valley sites, occupied somewhat later, provide evidence from earliest levels that inhabitants were essentially hunters and gatherers who relied on collected plant foods such as *Setaria,* amaranth, prickly pear (*Opuntia* spp.), avocado (*Persea* sp., probably wild), and mesquite (*Prosopis juliflora*) (Byers 1967). In subsequent levels, caches of *Setaria* seeds suggested that the inhabitants were cultivating this plant as well as planting domesticated peppers (*Capsicum* sp.), cotton (*Gossypium hirsutum*), squash (*Cucurbita* spp.), and agave (*Agave* sp.) (C. E. Smith 1967:232). No teosinte was recovered from the Tehuacán Valley sites. However, in a higher and more recent stratum, ca. 3500 B.C.

(Long et al. 1989), maize appears. The first maize at Tehuacán represents a fully domesticated cultigen, although it seems primitive in many aspects, i.e., the cobs are small, possess tiny kernels, and have long glumes (Benz and Iltis 1990). The major mutations giving rise to polystichous spikes and naked edible grains without hard fruitcases had already occurred by the time maize was introduced. It is likely that maize was domesticated elsewhere and introduced into the Tehuacán Valley sometime before or around 3500 B.C. By the time maize was introduced into the valley, the inhabitants were already involved in incipient horticulture. Maize seems to have been adopted quickly and became an important part of the subsistence strategy in subsequent periods. As this happened, Tehuacán farmers had larger and better maize cultivars, and as maize became more important in the diet through time, foods like *Setaria* and mesquite became less popular.

How did maize develop from the weedy grass with hard fruitcases to a cultigen that fed most Americans by the time Columbus arrived? There is only one way that maize came to be the cultigen that it is; the Archaic Mexicans, who were already familiar with agriculture, observed favorable phenotypes in teosinte that arose spontaneously through mutation, seized upon them and planted those seeds. The modifications they selected, larger spikes and naked kernels, would not have survived in the wild otherwise. To aid in its productivity, maize forms mycorrhizal associations with at least two species of fungi, *Glomus mosseae* and *Gigaspora margarita* (S. E. Smith and Read 1997:30).

QUINOA

Chenopodium quinoa was a major component of the Andean subsistence assemblage, especially at high elevations where it thrives in areas less frost-tolerant cultigens cannot. The earliest quinoa was reported from the Zaña site (6400–4000 B.C.) in northern Peru (Piperno and Pearsall 1998), although the antiquity of these seeds has been questioned (Rossen et al. 1996). Also, lines of botanical information indicate the cultigen originated in the southern Andes, then dispersed to the northern Andes and ultimately to coastal areas (Wilson 1990).

Other Archaic period evidence of Andean quinoa came from Lake Junin around 2500 B.C. (Hastorf 1993:114) and Pachamachay (Pearsall 1980). Holden (1994) described stomach contents from burials at the El Morro site in northern Chile that date from 2000 to 500 B.C. Numerous other prehistoric remains of this important cultigen have been found in Peru, Chile, and northern Argentina (Towle 1961). Possibly the association of this plant with humans was brought about during domestication of alpacas and llamas. Quinoa, one of the favorite foods of camelids, quite possibly began its association with humans when it volunteered in corrals from seeds transported in stomachs of llamas or alpacas (Kuznar 1993). Two subspecies of *Chenopodium berlandieri* were cultivated in Mexico (*nuttalliae*) and what is now the United States (*jonesianum*) and may have been domesticated independently (Wilson 1990).

POTATOES

Solanum tuberosum was, and still is, the principal staple crop of the mountainous regions and altiplano of the southern Andes. Evidence for the use of wild potatoes dates back to late Paleoindian–early Archaic times at Monte Verde (Ugent et al. 1987). The earliest domesticated potato remains, dated to 2000–1200 B.C., seem to come from the Casma Valley on the Pacific coast of Peru, a curiosity because they are highland plants (Ugent et al. 1982). Reports of potatoes from Tres Ventanas Cave, also on the coast of Peru, claim an early date of 8000 B.C., but these data have been challenged (B. Smith 1995).

Although the earliest archaeological potatoes come from the coast of Peru, botanical information suggests that the origin of the domesticate was in the mountain valleys of the Andes. The plant thrives above 3,350 m and proliferates exceptionally well in the puna zone of the Lake Titicaca region. Kitchen middens of early Andean hunter-gatherers could have provided the staging ground for the domestication of the potato (Ugent 1970), because the cold-hardy crop is ideally suited for this region of frequent frosts and short growing seasons. It was grown intensively during Tiwanaku times and even earlier through the use of irrigation and terracing. Potatoes are stored as *chuño,* or freeze-dried tubers, that are prepared by trampling moisture out of them and letting them dry in the sun followed by overnight freezing. Dehydrated potatoes store well and are an essential part of the Andean diet. They not only provide sustenance in lean times but also can be easily transported and have been traded for maize, pottery, fruits, and textiles with coastal inhabitants for centuries (Correll 1962). One reason for the success of potatoes are mycorrhizal symbionts (*Glomus* spp.) in the roots (S. E. Smith and Read 1997:30). But the potato, with its many varieties, is only one, albeit the most prominent, of Andean tuber crops. Other Andean root crops include oca (*Oxalis tuberosa*), ullucu (*Ullucus tuberosus*), and añu (*Tropaeolum tuberosum*).

MANIOC

Manihot esculenta, which probably originated in northeastern South America, was undoubtedly one of the most important crops in the Neotropical lowlands, yet it has been a paleoethnobotanically elusive cultigen. Literature regarding ancient manioc is clouded with many reports of poor archaeological documentation or questionable botanical identification. Problematic reporting of manioc has been decried by many authors (e.g., Heiser 1965; Cutler 1968; C. E. Smith 1968; DeBoer 1975; Ugent et al. 1986). One of the earliest reports of domesticated manioc comes from the Zaña Valley in northern Peru, where Piperno and Pearsall (1998) claim a preceramic date for manioc roots retrieved from below a house floor. As with the quinoa, however, AMS dates of associated materials indicate a historic or even modern origin of those plant remains (Rossen et al. 1996). Piperno and Holst (1997) also report "manioc-like" starch grains from grinding stones recovered from the Aguadulce rock shelter in a stratum that dates to 5000–4000 B.C. Another discovery of archaeological manioc, dating to as early as 1800 B.C., came from manioc starch granules found in the coastal Casma Valley of northwestern Peru (Ugent et al. 1986; Ugent 1994). Small stone chips, possibly from a manioc grater (2100–1600 B.C.) were found at Parmana in Venezuela (Roosevelt 1984). Similar concentrations of stone chips, also likely from a manioc grater, were found in middle Formative deposits (ca. 900 B.C.) at the Yarumela site in central Honduras (Lentz et al. 1997). Elsewhere in Central America, casts of manioc tubers were identified at the Cerén site (ca. 590 A.D.) in El Salvador (Lentz et al. 1996). Callen (1967) reports manioc remains from Santa Maria times (ca. 900–200 B.C.) at Coxcatlan Cave, Tehuacán Valley, Mexico. Towle (1961) cites many examples of dried manioc roots from Early Horizon coastal Peru (900–200 B.C.) to more recent times, as well as references to ancient pottery and textiles with clear depictions of manioc roots from the Nazca, Moche, Chimu, and other early Peruvian cultures.

Much discussion has been generated, both archaeologically and ethnographically, about the distinction between sweet and bitter manioc with reference to cyanide-containing properties of roots, but studies have shown cyanide contents are actually quite variable, do not correspond to any morphological characteristics, and probably are more a function of culturally associated belief systems than actual toxicity (Nye 1991). Furthermore, elaborate processing procedures are more related to the desired end product (manioc flour) than are required for purposes of detoxification (Nye 1991). Future archaeological discussions regarding ancient manioc should follow in light of this understanding.

TREE CROPS

Many tree fruits were of great importance to the Precolumbian inhabitants of both North and South America. In what is now the midwestern and eastern United States, naturally occurring nut and fruit trees, such as hickories (*Carya* spp.), chestnuts (*Castanea* spp.), persimmons (*Diospyros* spp.), beech (*Fagus americana*), wild plum (*Prunus americana*), hackberries (*Celtis* spp.), and oaks (*Quercus* spp.), were important food sources from early Holocene times until historic times, even after the introduction of maize and the adoption of other cultigens (C. E. Smith 1986; Meltzer and Smith 1986). Although these trees and other representatives of eastern forests may have been encouraged by not cutting them down or by clearing away competing species less useful to humans, none were really domesticated.

Notwithstanding considerable obstacles, e.g., seeds that do not breed true and characteristically long generation times, ancient Americans were successful at domesticating a number of excellent fruit-bearing trees. One of the most important, at least economically if not nutritionally, was the cacao or chocolate tree (*Theobroma cacao*). Although the plant originated in northern South America (Young 1994; Schultes 1984), some believe it was domesticated by the ancient Maya (e.g., Krickenberg 1946). Yet, seeds lose their germinating power after two weeks (León 1959) and do not travel well, so it seems hard to imagine that long-distance trade was the best explanation for the introduction of cacao in Mesoamerica. Alternatively, it has been proposed that cacao was transported as small seedlings from South America to Central America (Stone 1984). This explanation seems less parsimonious than a down-the-line movement of seeds from a plant initially cultivated in South America, probably for the delicious aril or pulp surrounding the seeds. In addition, with a down-the-line exchange of germ plasm, the crop would have been less likely to outdistance its mycorrhizal symbionts. However cacao arrived in Mesoamerica, the Maya certainly developed and improved the tree crop from South American seed stock and created new culinary dimensions, such as the exquisite beverage derived from the seeds.

Another domesticated tree, cashew, originated in southern Brazil (Mitchell and Mori 1987) yet somehow got transported up to Central America by middle Formative (900–400 B.C.) times (Miksicek 1991; Lentz et al. 1997). Other domesticated trees in Neotropical lowland areas included ciruelas (*Spondias* spp.), anonas (*Annona* spp.), papaya (*Carica papaya*), avocado (*Persea americana*), sapodilla (*Manilkara achras*), zapote (*Lucuma mammosa*), and guava (*Psidium guajava*). Palms were enormously important as well, especially coyol (*Acrocomia aculeata*), cohune (*Attalea cohune*), cocoyol (*Bactris major*), peach palm (*B. gasipaes*), pacaya (*Chamaedorea tepejilote*), corozo (*Elaeis oleifera*), and babassu (*Attalea speciosa*). Of these, probably only peach palm and pacaya were truly domesticated. The others were encouraged and cultivated, and many of them, such as coyol, had their seeds moved and thus their range enlarged by humans, but they remained essentially wild plants, fully capable of surviving on their own. Other trees in the wild-but-encouraged category include black zapote (*Diospyros ebenaster*), inga (*Inga* spp.), mesquite (*Prosopis* spp.), ciruela de fraile (*Bunchosia armeniaca*), nance (*Byrsonima crassifolia*), acerola (*Malpighia punicifolia*), and ramón (*Brosimum alicastrum*).

From the list of plants in table 4.2, we can observe a number of interesting aspects of plant-human interactions. Most obvious is the widespread dissemination of plant species useful to humans. Many species had small ranges initially that became greatly expanded by human action. The examples of cacao and cashew described above help illustrate an important point about Precolumbian trade interactions. Many archaeologists, who like to think of the groups they work on as arising sui generis without outside influences, tend to downplay the diffusion of artifacts, trade goods, and especially ideas in Precolumbian America. Dissemination of plant germ plasm, however, clearly shows humans were transporting seeds and knowledge of plants from one region to another and in some cases from very early times. This undoubtedly occurred in conjunction with the trade of other commodities; there is no evidence to suggest that Precolumbian traders specialized in unusual crop seeds only. Maize is an obvious example of a well-traveled crop that from its limited original range in western Mexico made its way as far north as New England and Canada and as far south as temperate South America in Argentina long before the first European ever set foot in the New World.

Another observation from table 4.2 is that there is much we do not know about a number of important domesticates. For some plants we can only guess as to the wild progenitors, and for others we have no idea. This lack of knowledge can be solved by focusing intensive collection in areas of suspected origins. Newly developed molecular techniques will help to sort out answers, if adequate plant material can be obtained from regions whose flora is poorly known. Moreover, archaeologists interested in the origins of agriculture should investigate sites in the home range of the ancestral populations to find early evidence of plant domestication.

WEEDS AND PIONEERS

If domesticated plants were so widely disseminated, what were the plants that were replaced by the spreading wave of human-centered trophic webs? For an indication of the geographic areas and vegetation types that were most heavily impacted, the reader should look to the essays on vegetation in this volume. Although there were many plants whose numbers were diminished by human influence, there were others that proliferated in the wake of human-centered trophic webs, and these are generally referred to in agronomy circles as weeds. There are a number of weedy genera that spread throughout the hemisphere, ready to move into a trash heap or abandoned agricultural plot when the opportunity arose. Most of these weeds share an *r* selection strategy with many of the first domesticates, and in fact, some are congeners with early domesticates. Native panamerican weedy genera include the numerous taxa found in table 4.3. For the most part these fast-growing herbaceous plants act as early colonizers in successional sequences, soon followed by shrubs and pioneer trees that may eventually shade out herbaceous invaders.

Pioneer trees and shrubs tend to grow quickly and reach maturity within a couple of decades. Examples of the woody pioneers in southeastern North America are listed in the first part of table 4.4 (Harper 1944; Radford et al. 1968), while woody pioneers

TABLE 4.3. NATIVE PANAMERICAN WEEDY GENERA

Family	*Common Name*	*Genera*
Amaranthaceae	amaranth	*Amaranthus*
Asteraceae	sunflower	*Ambrosia* *Aster* *Bidens* *Eupatorium* *Mikania*
Chenopodiaceae	pigweed	*Chenopodium*
Commelinaceae	spiderwort	*Commelina*
Convolvulaceae	morning glory	*Ipomoea*
Cyperaceae	sedge	*Carex* *Cyperus* *Eleocharis* *Fimbristylis*
Euphorbiaceae	spurge	*Phylanthus*
Leguminosae	bean	*Cassia* *Desmodium* *Crotalaria*
Malvaceae	mallow	*Sida*
Onagraceae	evening primrose	*Ludwigia*
Passifloraceae	passion flower	*Passiflora*
Poaceae	grasses	*Andropogon* *Cenchrus* *Panicum* *Paspalum* *Tripsacum*
Phytolaccaceae	pokeweed	*Phytolacca*
Smilacaceae	catbrier	*Smilax*
Solanaceae	nightshade	*Physalis* *Solanum*

Source: This was prepared by cross-checking lists of weedy plants from North America (Harper 1944; Radford et al. 1968), Central America (Garcia et al. 1975; Lentz 1989), and South America (Myint 1994).

TABLE 4.4. WOODY PIONEERS

Southeastern North America	*Central America*	*Lowland South America*
Aesculus pavia	*Acacia cookii*	*Alchornea triplinervia*
Alnus serrulata	*A. pennatula*	*Aparisthmium cordatum*
Catalpa bignonioides	*Acrocomia aculeata*	*Astrocaryum huicungo*
Celtis spp.	*Ardisia revoluta*	*Bixa orellana*
Cephalanthus occidentalis	*Bactris major*	*Casearia macrophylla*
Diospyros virginiana	*Calliandra emarginata*	*C. ulmifolia*
Ilex vomitoria	*Cassia fistula*	*Cecropia* sp.
Liquidambar styraciflua	*C. grandis*	*Coccoloba* sp.
Morus rubra	*Cecropia peltata*	*Cordia* sp.
Pinus echinata	*Diospyros cuneata*	*Doliocarpus dentatus*
P. taeda	*Genipa caruto*	*Geonoma* sp.
Platanus occidentalis	*Gliricidia sepium*	*Inga quaternata*
Populus deltoides	*Guazuma ulmifolia*	*Isertia hypoleuca*
Prunus angustifolia	*Inga* spp.	*Jacaranda copaia*
Rhamnus caroliniana	*Iresine arbuscula*	*Miconia tomentosa*
Rhexia spp.	*Leucaena brachycarpa*	*Pharus virescens*
Rhus glabra	*Pinus caribaea*	*Pollalesta discolor*
Sambucus canadensis	*Saurauia villosa*	*Rinorea racemosa*
Sassafras albidum	*Solanum atitlanum*	*Sorocea hirtella*
	Spondias mombin	*Vismia angusta*
	Thevetia ovata	
	Trema micrantha	

in Central America are listed in the second section (Lentz 1989), and pioneer woody plants from the Amazon region described in a study of forest regrowth (Denevan and Treacy 1987) can be found in the third section. A quick glance at each of the three sets of plants reveals some overlap in genera among the three regions, but overall the lists reflect the division between Holarctic and Neotropical floras (see Greller, this volume). Central America is the meeting ground between the two floras and so has representatives from both. One common genus in all the Americas is *Pinus,* part of the Holarctic flora, whose range extends from southeastern North America across Central America and even into the highlands of South America. It seems likely that fire climax pine savannas developed as a result of repeated anthropogenic burning in several areas (Perry 1991). All of the plants listed in this section are pioneer species that are adapted to the kinds of disturbances found in nature and created by humans. Although some may be viewed as intrusive weeds, most, as important trophic web components, are valuable to humans as sources of food, medicines, and construction materials; as hosts for nitrogen fixers; and as part of the gene pool for domesticates through periodic hybridization and introgression.

SUMMARY AND IMPLICATIONS

The process of creating human-centered trophic webs in the Americas, which included domesticated plants, animals, weedy species that adapted to human disturbance, and associated symbionts, began some time prior to 8000 B.C. To date, the earliest cultigen (*Cucurbita pepo*) positively identified as such was unearthed in the Oaxaca Valley. Other plants were domesticated in distant regions, but whether these were independent events or the result of idea diffusion is hard to say. Sometime before 500 B.C. in southern Mexico, domesticated maize, beans, and squash came together, probably along with roots and other crops, as an agriculturally and nutritionally complementary system that formed the economic foundation for mesoamerican civilizations. Trade networks exchanging bird feathers and other exotic commodities for turquoise in western Mexico carried mesoamerican germ plasm to southwestern North America sometime before 1500 B.C. (Riley et al. 1990), where vibrant cultural traditions developed along with crop varieties adapted to arid lands.

Maize did not arrive in the Eastern Woodlands of North America until some time around A.D. 175 (Chapman and Crites 1987). It might have entered the region from Mexico via the Southwest, or the Gulf coast, while others suggest a Central or South American introduction via the Caribbean (Riley et al. 1990). However it arrived in North America, it was not used extensively for many centuries. Before maize, eastern North American cultures were dependent on a set of locally domesticated or quasi-domesticated plants, i.e., goosefoot, knotweed, maygrass, little barley, marsh elder, sunflower, and squashes, along with other wild plant and animal foods. It has been asserted that locally domesticated goosefoot, marsh elder, squash, and sunflower represent original domestication events that apparently took place within a few centuries (2500–2000 B.C.) of each other (B. Smith 1995). In a recent discovery, early sunflower evidence was unearthed from pre-Olmec deposits in Tabasco, Mexico, a find that brings into question the North American domestication of sunflower. Maize cultivation, along with beans and squash, became important around A.D. 800, and Mississippian societies flourished.

In the Neotropical lowlands of Central and South America, domestication of manioc and other root crops began at least by 2000 B.C. and probably much earlier. Although some have described the Neotropical lowlands, particularly the Amazon region, as lacking in resource potential (Meggers 1971; Gross 1975; Ross 1978; Harris 1984), others (Lathrap 1973; Roosevelt 1998) have pointed to archaeological evidence that demonstrates the presence of substantial prehistoric settlements along the floodplains of the Amazon, which survived on manioc, maize, squashes, palms, fruit trees, and other plant food sources as well as the bounty of the forest and riverine fauna. Balée (1989, 1992, 1993) suggests the settlement pattern we now observe in the Amazon basin is actually a cultural artifact, and in the Precolumbian past, human populations were large enough to create "anthropogenic forests." Balée's assessment seems plausible for certain parts of Amazonia, such as the eastern várzea areas, where relatively large populations settled. In any case, the importance of the Neotropical lowlands in the development of domestication and cultural evolution in the Americas is gaining wider recognition (Piperno and Pearsall 1998).

In the Andes, agricultural economies, based largely on plant foods derived from quinoa, potatoes, and other root crops, as well as domesticated animals, viz., the llama, alpaca, and guinea pig, began around 3000–2000 B.C. (B. Smith 1995). Maize, beans, squash, and peppers, which grow less well at high altitudes, were more marginal contributors in the mountainous regions. However, Hastorf and Johannessen (1993) point out that even though maize may have been introduced to the region around 2000 B.C., it remained in a role of secondary crop until about A.D. 500, when the use of maize beer, or chicha, took on a role in ritualized feasting. From then until historic times the use of maize in ceremonial activities accounted for its major use in the region.

In summary, arrays of wild and domesticated plants with their microbiological symbionts and multicellular animals were incorporated into trophic webs throughout much of the temperate and tropical Americas. These webs supported stratified societies that modified their surroundings in a variety of ways by favoring useful species, through vegetation replacement, through introduction of domesticated animals, and in many cases through earth-moving activities that ultimately transformed the landscape of the Americas in distinctly human ways.

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