

## Some aspects of avocado (*Persea americana* Mill.) diversity and domestication in Mesoamerica

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**Abstract** Avocado (*Persea americana* Mill.) is a major tropical fruit, with origin in Mesoamerica area. Avocado is a very variable species and taxonomically poorly understood. It has been grown in the Neotropics since ancient times and it seems that the domestication of this tree in Mesoamerica started before other annual crops. In addition, it seems that much of avocado diversity as ecological differences, were originated as a result of cultural diversity. In view of this, avocado represents an interesting model to study domestication of tropical trees and develop forest management and germplasm conservation strategies. At present time, *P. americana* is worldwide distributed with Mexico as the main producer. However, there are some aspects on the origin, dispersion, and domestication of the species that

remain to be answered. In this paper, we present a survey of these issues from the earliest to present time in Mesoamerica.

**Resumen** El aguacate (*Persea americana* Mill.) es una importante fruta tropical, originaria del área de Mesoamérica. El aguacate es una especie altamente variable y su taxonomía aún no ha sido totalmente definida. El aguacate se ha desarrollado en el Neotrópico desde tiempos antiguos y es posible que su domesticación en Mesoamérica se iniciara antes que otras plantas anuales. También es probable que en gran medida su diversidad se originara además de las diferencias ecológicas, también como resultado de la diversidad cultural. Debido a esto, el aguacate representa un modelo interesante para estudiar procesos de domesticación en árboles tropicales y desarrollar estrategias de manejo en bosques y conservación del germoplasma. Actualmente, *P. americana* está distribuida en todo el mundo y México es el principal productor. Sin embargo, algunos aspectos del origen, dispersión y domesticación de la especie no han sido clarificados. En este artículo presentamos una investigación sobre estos aspectos, desde tiempos antiguos hasta el presente en el área de Mesoamérica.

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## Introduction

The history of human subsistence at the end of the Pleistocene has been characterized by the presence of hunter-gatherers, however, at some time between 8,500 and 2,500 B.C. the domestication of plants and animals arose independently in at most nine areas of the world (Diamond and Bellwood 2003). The evidence to document domestication processes of plants has been based mainly on grasses and annuals (wheat, barley, maize, beans, etc.), and little attention has been paid to the domestication of trees, especially in tropical rain forests in the Americas (Simons and Leakey 2004). With the exception of temperate fruit trees, tropical trees are far more neglected than agricultural crops and only about 40 taxa have genetic improvement programs under way with no more than 60 years of tradition (Barnes and Simons 1994).

Trees have played a special role in the development of many cultures, where certain tree species have been considered sacred (Dafni 2006). In this regard, there are reports for tree species that have been domesticated since remote times in the Old World. Among these species are the sycamore tree (*Ficus sycomorus* L.) and the date palm (*Phoenix dactylifera* L.) (Dafni 1992; Kevan and Phillips 2001). In addition, Kislev et al. (2006) have suggested that *Ficus carica* L., a parthenocarpic fig, was the first domesticated plant of the Neolithic Revolution, even before the grasses, by about 9,400 B.C. However, as all parthenocarpic fig types can produce seeds, according to Lev-Yadun et al. (2006) it seems an ambiguous proposal that this tree domestication predated grain crops in the Near East.

In the Neotropics, above all in Mesoamerica, trees have played a special role in the development of cultures. In this area, one of the trees with an ancient history of interaction with humans is avocado (*P. americana* Mill.). Seed archaeological remains of this tree were found in Tehuacan valley, Puebla, dated 8,000–7,000 B.C. and possibly domesticated since 6,400 B.C. (Smith 1969). This finding suggests that avocado is one of the first trees domesticated in the Neotropics and represents a very important species to understand patterns of domestication and evolution of neotropical trees, specially in areas of high biodiversity.

Nowadays, avocado is distributed worldwide with a global production in 2005/2006 estimated at

1,437,000 tonnes, with Mexico as the main producer (Foreign Agricultural Service, USDA 2006). However, in spite of the old relation between avocado and humans there is still a lack of basic information regarding the origin, centers of domestication, pre-Hispanic use, and management of avocado in the forests where it grows.

The purpose of this paper is to present an overall scope of the origin, migration, and domestication of avocado and shed some light on these important issues that need to be addressed in order to understand genetic diversification, not only for avocado, but in other tropical trees, specially species under human selection.

## Taxonomic background

*Persea americana* Mill. belongs to the Lauraceae, one of the oldest known flowering plant families (Renner 1999). It is a very variable family with about 50 described genera and an undetermined number of species ranging from 2,500 to 3,000, distributed mainly in the tropical and subtropical regions all over the world (Rohwer 1993). However, evidence from the gen *matK* suggests a very low-genetic divergence within the family (Rohwer 2000). The Lauraceae family and specially the genus *Persea* have a bad reputation among taxonomists as being difficult to classify (Lorea 2002). For example, the *Persea* genus has been recognized as having two subgenera, *Persea* and *Eriodaphne* (Kopp 1966); but recently, Campos-Rojas et al. (2007) in a phylogenetic analysis of the genus *Persea*, based in 40 morphological characters, have proposed that *Eriodaphne* and *Persea* should be considered as independent genera.

The confusion on the taxonomic circumscription of the genera have been the variability of the floral parts and the density of the indumenta, characteristics on which specialists base the description of species (van der Werff 2002). The use of these characters leads to confusion because floral parts characters usually overlap among species and indumenta have been proved as a very subjective character (van der Werff 2002).

Avocado, as most of the members of the Lauraceae family, is a very variable species (Knight Jr 1999) and there are local variations that have resulted in different ecological races or varieties. Three of these

varieties are widely recognized by horticulturalists: the Mexican (*P. americana* var. *drymifolia* (Schlecht. et Cham. Blake), the Guatemalan (*P. americana* var. *guatemalensis* L. Wms.), and the West Indian (*P. americana* Mill. var. *americana*) (Berg and Ellstrand 1986; Berg 1992; Lavi et al. 2003). In addition to these three widely recognized varieties of *P. americana*, there are reports for other types, among them var. *nubigena* (L. Wms.) Kopp (Kopp 1966) and var. *costaricensis* Ben-Ya'acob (Ben-Ya'acob et al. 2003). Besides, there is a very close species in terms of morphology of flowers, fruits, and domestication: *P. schiedeana* Nees. Some of the reasons for considering *P. schiedeana* a different species are that it has shorter pedicels (to 8 mm long), the terminal buds are protected by uniform pubescent bracts, and its leaves are narrow. According to van der Werff (2002) much of this variation can be attributed to the great diversity of environments characterizing the dispersion area. In this view, it is not clear if *P. schiedeana* is just part of the variation of *P. americana* or effectively a different species. Because of this, in order to clarify the avocado diversity, these studies should integrate aspects as its origin, dispersal, and history.

### Early origin and dispersal

In regard to the avocado origin, according to archaeological evidence, the early origin of the Lauraceae family has been situated, as well as other angiosperms, since the Early Cretaceous (144–94 million years ago) in west Gondwana. From there, avocado ancestors migrated via Gondwana–Laurasia–North America (Scora and Berg 1992). In North America, Lauraceous members (*Persea* ancestors) lived during the late Cretaceous (94–70 million years ago) and during the Early Tertiary (65–33 million years ago) in areas considered as semi-tropical climate through the Rocky Mountains and along the Pacific Coast from California to Alaska. But, during the climatic changes in the Pliocene (5.3–1.8 million years ago), most of these plants did not survive (Schroeder 1968; Millar 1996). However, the relationship among the leaves fossils of *Persea* found in the semi-arid areas of northern Mexico with the ones found in California (Schroeder 1968) suggest that some of the plants living in North America migrated southward.

The early avocado dispersal cannot be determined using historical literature and the mechanisms for long-distance dispersal remain unknown. It seems that early Lauraceae dispersal has been accidental, such as transport of seeds within the soils or water and latter facilitated by animals moving propagules and seeds (Hodkinson and Thompson 1997; MacDougall 2003; Renner 2004). Among these animals are the big mammals, such as the giant ground sloths, which were common in America during the ice ages and had been reported as avocado dispersers (Diamond 1999; Barlow 2002). It is possible, given the avocado seed which has only a thin oily flesh to attract dispersers, that ground sloths with relatively small, blunt teeth could have swallowed the whole fruit and excreted the seed in dung, ready to sprout (Barlow 2002; Renner 2004). With this probable spreading way, it seems that *Persea* members reached Mesoamerica during the climatic fluctuations at the Pleistocene (1.6–0.01 million years ago), where they proliferated and differentiated along the diverse habitats available in the area (Berg 1995; Chanderbali et al. 2001; Renner 2004). When humans arrived to America about 13,000 years ago (Diamond 1999), they became an increasingly important mechanism of avocado dispersal (Barlow 2002). At this time humans lived as hunter-gatherers (Simpson and Ogorzaly 1995) and probably they dispersed plants as they expanded southward, mainly for spontaneous growth from leftovers (Weirsum 1997a). When human groups started living in a sedentary way of life and agriculture began, people could engage in activities other than food procurement. Activities as commerce, administration, and warfare became important to them (Gepts and Papa 2002) and trade with plants in pre-Hispanic Mesoamerica was very common. In this scenario, it is possible that after initial domestication, avocado was widely dispersed through the commercial routes, not only all over Mesoamerica but even to Peru. In this way, when Spanish arrived to America the avocado was spread from Mesoamerica to Peru (McPherson 1955; Popenoe 1963; Takashi 1968).

### Diversity

Since avocado dispersal in America occurred in a north–south direction, its diversity can be explained in terms of the evolutionary change to adapt to

diverse ecological conditions as day lengths, seasonalities, habitats, and diseases for different latitudes (Diamond 2002). However, avocado diversity should not only be related to ecologic conditions. Mesoamerica has been an area with a great cultural diversity (Toledo et al. 2001), therefore, it is probable that much of avocado diversity, in addition to ecological differences, was originated as a result of human intervention (Gama-Campillo and Gomez 1992; Perales et al. 2005).

An important source for understanding local avocado variations in Mesoamerica is the chroniclers of the pre-Hispanic time. One of these chroniclers was Friar Toribio de Benavente. In his book “Historia de las Indias de la Nueva España y de Memoriales,” written in 1542, he described three types of avocado that could correspond with the actual Mexican, Guatemalan, and American varieties (Benavente de 2003).

Friar Bernardino de Sahagun, recognized as the main chronicler of the pre-Hispanic period, wrote the “Historia de las Cosas de la Nueva España” in 1547. In this book he also described three different types of avocado and the Aztec names given to them. He mentioned a tree named *ahuacatl* o *ahuacacuahuitl* with dark green leaves and a black fruit in the outside and green to white inside. Other *ahoacates* named *tlacazolahuacatl* are as the former but big and a third type of *ahocates* named *quilahuacatl* is green outside and very good to eat (Sahagun 2002). Acosta, in 1590, made a difference between the avocados in Mexico and the *paltas*, the name given to avocado in Peru. In this regard, he wrote: In Peru the *paltas* are big with hard skin, peeling readily. In Mexico most of them are small with thin skin that peels like the apples (Acosta de 1985). It is interesting the way Friar Bernabe Cobo, in 1653, not only described the three avocado varieties, but situated them geographically. He wrote: The *palta* in some regions become as big as a small squash or large citron, the varieties of the province of Yucatan in New Spain (Mexico) being of this class. The *palta* has a thin skin. It has the largest seed that I have ever seen in any fruit, either in the Indies or Europe. Between the seed and the rind is the meat, slightly thicker than one’s finger except at the neck where it is very thick. It is of whitish green color, tender, buttery, and very soft. The second kind is a large, round one which is produced in the province of Guatemala, and which does not have as

smooth skin as the first. The third is a small *palta* found in Mexico, which in size, color, and form resembles a breva fig; some are round and others elongated, and the skin is as thin and smooth as that of a plum (Cobo 1956).

It is evident that the avocados described by Benavente, Sahagun, and Cobo correspond with the Mexican, Guatemalan, and West Indian varieties recognized actually. Each one of these varieties has some distinguishable morphologic, ecologic, and molecular characteristics and had been described based on their morphologic and ecologic characteristics, among others by Berg and Ellstrand (1986) and Knight Jr (1999) as follows:

1. The Mexican type has a delicate skin, the seed is large and often objectionably loose in the cavity and fruits are generally smaller than is commercially desirable. This type is adapted to high elevations, has the greatest resistance to cold in the species and the high-oil content with associated rich nutty flavor.
2. The Guatemalan fruit averages the highest in horticultural quality of the three races. The skin is thicker, the seed is usually smaller, and it is tight in the cavity. Not all Guatemalan avocados have this thick or woody skin. Another invaluable advantage of Guatemalans is their much greater length of time to maturity. This not only provides a later harvesting season, but hybrids with the two earlier-maturing races bridge the race maturity gap; in a climate like California, fruit is therefore picked commercially year-round. The Guatemalan avocados are adapted to high elevations and have the ability to survive cold weather in good condition.
3. The West Indian type has the greater salt and chlorosis tolerance. This type is well adapted to lowland tropical regions, and its hybrids with Guatemalans bridge the two harvesting seasons, while combining good Guatemalan quality with good West Indian adaptation to tropical climates.

In addition, Nubigena type has been described by Kopp (1966) based in leaf characteristics as form, pubescence and texture, latter Williams (1977) described the fruits of Nubigena as always small, perhaps 3–4 cm in diameter, globose or rarely subpyriform and green. The flesh is sparse and rarely more than 5 mm thick. Ben-Ya’acov et al. (2003)

described the Costaricensis avocado as a variety with a round and small fruit, about 4 cm in diameter. The typical fruit has a very small amount of flesh, poor quality, and ripens in September. The seed is relatively big and frequently used as a rootstock source.

A comparison of the Mexican, Guatemalan, and American varieties has been made by Berg (1992) and recently, Campos-Rojas et al. (2007), based in morphological characters, made a phylogenetic analysis, of “*Persea* avocados.” However, not only the morphological and ecological evidence supports the distinctiveness of these varieties or ecological races of avocado. There are also molecular studies that have differentiated the three varieties.

The genetic relationships of avocado have been studied with Restriction Fragment Length Polymorphism (RFLP) analyses. Furnier et al. (1990) proposed, using RFLP analyses in cpDNA and nDNA that the Guatemalan variety was an inter-specific hybrid between *Persea steyermarkii* Allen and *P. nubigena* (L. Wms.) Kopp. They also found that the Mexican variety was closely related to *P. floccosa* Mez. Later, Davis et al. (1998) also using RFLPs, found three mayor groups of cultivated avocado and additional clusters placed between these mayor groups, indicating a hybrid origin. In addition, Fielder et al. (1998) using randomly amplified polymorphic DNA (RAPD) studied and confirmed three groups representing the three varieties of avocado. Furthermore, Mhameed et al. (1997), using minisatellite DNA markers, suggested that the Guatemalan and West Indian varieties are more similar to one another than either is to the Mexican one.

Later, Schnell et al. (2003) using microsatellite markers observed a general concordance between the three varieties and the clusters obtained from their molecular data. Ashworth and Clegg (2003), also using microsatellites presented two unrooted neighbor-joining phenograms with three clusters likely corresponding to the three varieties and intermediate clusters grouping genotypes of presumably hybrid origin.

However, the genetic relationships of avocado have been complex. Owing to the importance of hybridization in avocado, genetic relationships present a reticulate evolution (Clegg et al. 1993). Because of this, the genealogical relationships within the species are obscure and the origin and domestication process are not clear.

Moreover, according to different authors, each one of these racial ecotypes has been related to different origin centers (Heiser 1965; Kopp 1966; Williams 1977; Storey et al. 1986). As these centers are in relatively close proximity it seems that in addition to geographic isolation, the out breeding behavior of the species and human intervention have been important factors in the development of avocado variation (Gama-Campillo and Gomez 1992).

Because the results of different studies have been diverse, it has been difficult to agree on avocado diversity and opinions are diverse, according to the author point of view. Anderson (1960) has pointed out that *Persea* includes a number of wild species representing the progenitor(s) of cultivated species or could be an escape from cultivation that has reverted to wild or semi-wild condition. Because the lack of useful characters to distinguish among varieties and related species, Gama-Campillo (1992) included the varieties and related species in the “americana complex.” And van der Werff (2002) has considered that variation in *P. americana* can be attributed to the process of cultivation and prefer to accept *P. americana* on a wide sense and ignore the cultivated races of this species.

From this perspective, avocado diversity should be analyzed not only by the geographical side, but as the result of the domestication processes by the different cultures that have lived in the distribution area of the species. It is evident that the purposeful selection by different cultural groups has modified avocado diversity.

## Domestication

Archaeological records are essential to begin to understand the spatial and temporal patterns of initial domestication and subsequent diffusion of domesticated plants (Smith 2005). For the avocado, the first archaeological evidence of human contact with this tree are the cotyledons found at Coaxcatlan, Puebla dated from 8,000 to 7,000 B.C. (Smith 1966). At this time, humans were mostly foraging on the natural local flora and it is likely that these groups exploited some of the plants that were abundant in their immediate surrounding and required minimal processing prior consumption. These groups of people should select a number of plants among the great

variety available (Betz 1999) including the avocado, chili, and squash (Mac Neish 1964; Smith 2005).

In this regard, avocado selection from its wild ancestors in ways making it more useful to humans could be started with people occupation of available habitats next to permanent gardens, orchards and pastures, instead of migrating to follow seasonal shifts searching for wild food supplies (Diamond 2002).

By 7,500–4,500 B.C. the climate in Central Mexico was warm and moist and hence hospitable to local plants such as *Prosopis*, *Agave*, *Opuntia*, *Setaria*, *Spondias*, *Syderoxylon*, *Cyrtocarpa*, and *Persea* (Buckler et al. 1998). Even when grasses and annuals were also available, they have not been reported in this period as foodstuffs (Betz 1999). Therefore, it is probable that human groups living in this area started exploitation, propagation, and care of the former species, specially when they found that if you drop a seed in the ground a plant comes up (Mac Neish 1964).

Later, when climate became variable and dryer around 4,500–2,000 B.C., avocado became rare and cultivation, probably as forest gardens, would have been necessary to maintain this favored food (Weirsum 1997b; Buckler et al. 1998; Diamond 1999). In this view, avocado domestication could be started as a simple way to promote this tree conservation as it has been proposed for other crops (Ellstrand and Marshall 1985).

Once people started harvesting the avocado fruits, they should have started practicing selection for large fruit and also improved avocado quality (Smith 1966, 1969) as it has been shown by the full progression of sizes observed in the seeds found at Tehuacan valley (Smith 1966). Even when a large jump was observed until 900–200 B.C., it is possible that because of the long juvenile period and life cycle of the avocado tree, the results of selection were not readily apparent until then (Smith 1969) and avocado domestication started before this jump in size was observable. These data indicate that the avocado tree domestication could have started in Mesoamerica before annual crops when early humans consumed and, in doing so, modified the wild avocado. Later, the selected fruits were dispersed in some areas of Mesoamerica.

One example of this early dispersion is the seeds found in the Oaxaca valley around 1,200 B.C. These seeds are of similar size and shape than the ones found in Tehuacan valley, suggesting that people

from Coaxcatlan dispersed their avocado selected fruits to Oaxaca, where avocado fruit size had not been improved (Smith 1969).

In addition, there are early Mesoamerican cultures that, being avocado consumers and efficient in food production could have domesticated for alternative purposes, the plants they already knew, resulting in different appearing crops (Diamond 2002).

Under those conditions, it might be reasonable that the Mokayas (1,800 B.C.), one of the first cultures of Mesoamerica and considered as the forerunners of the Olmec and the Maya cultures started the early avocado domestication, even before annual crops. Data supporting this proposal are: the Mokayas lived in the Soconusco, an area where avocado has been a naturally growing tree (Debouck and Ferla 1995). By this time, the early agricultural groups were cultivating avocado (Mac Neish 1964). Besides, Taube (2004) has suggested that because corn ears recovered from that area are small and unproductive and the chemical analysis of Mokaya human bone collagen revealed that plants as maize, with a C-4 photosynthesis pathway, were not part of the local diet, the maize seems not to have been the main food for these people. Since avocado was a common tree in the area and it represented an energetic and strong food in their diet, it seems that this tree domestication started when these people took care, selected, and propagated the avocado as an option in food production. Moreover, as the Mokayas were the forerunners of the Olmec and Maya cultures, then they could inherit this knowledge to these people that also lived in an area where avocado was naturally growing.

There is evidence that by 1,500–900 B.C. avocado was cultivated by the Ajalpan people (Mac Neish 1964). On this view, it could be that Olmecs (1,600–500 B.C.) not only domesticated avocado but were an important link in the avocado spread chain.

In Mesoamerica, since that time, there has been a wide network for commercial exchange (Ortiz and Rodriguez 2000). There are indications for Olmec contact with the Papayecas in Honduras around 1,200–1,000 B.C., a time that coincides with the avocado seed remains found at Rio Claro excavations (Healy 1978); suggesting that Olmecs not only have been avocado domesticators but could have dispersed it through their wide commerce network.

In the other hand, it is also known that avocado has been grown in the Maya region at least since 3,400

B.C., and it could have been selected by local human groups since earlier times (Colunga-GarcíaMarín and Zizumbo-Villareal 2004). Practices as the introduction, selection, protection, and cultivation have been performed by the Mayas, who brought wild trees into homegardens and selected avocado for cultivation (Gama-Campillo and Gomez 1992).

It is important to mention that the Maya brought the avocado tree into homegardens and orchards not only as a food source but as part of their culture and mythology, with an important religious meaning (Herrera-Castro et al. 1993). Mayas believed in the rebirth of their ancestors as trees. This explains why these people surround their houses with fruit trees. The metaphor of the ancestral orchard showing the rebirth of the ancestors as trees and the importance of avocado for this culture is illustrated on the king *Hanab-Pakal's* sarcophagus in Palenque, Chiapas. On the sides of this sarcophagus there are ten ancestors represented by ten figures emerging from a crack in the earth along with a fruit tree. One of them is the figure of Lady *Olnal* emerging with an avocado tree. These figures constitute a forest growing around the coffin of the king, but it is not a wild forest. Instead, the ancestors emerge with fruit trees that the Maya grew and tended around their houses (Schele 1974, 1998).

Other culture that also seems have been avocado domesticators are the Toltecs (1,000–1,200 A.D.). They lived in a town named Aculma, an important pre-Hispanic area where avocado was grown, as is mentioned in the *Suma de visita de pueblos* (Paso y Troncoso 1905). This document consists of an inventory of goods from 907 towns in central Mexico, obtained between 1531 and 1544. In this inventory, Aculma has been cited as a town paying tribute to Aztecs, among other trades, with avocado.

Other important pre-Hispanic area for avocado domestication could be northern South America. There is archaeological evidence for the presence of avocado seeds in the Peruvian Pacific coast about 1,500 years B.C. (Heiser 1979). In regard to the presence of avocado in this area, Wolters (1999) suggests that people of the Valdivia, an ancient Ecuadorian culture presumably brought avocado to western Ecuador and neighboring northern Peru from Southern Mexico since 1,450 B.C. Since they were known by their trips by boat or raft along the coasts from their home to southern Mexico.

In addition, the avocado presence in the Inca warm valleys has been documented by de la Vega (a Spanish chronicler). In his book *Comentarios reales de los Incas*, published in 1605, he mentions that avocados were not cultivated in Peru many years before Spanish arrival. De la Vega describes how avocado was brought to the Inca lands when *Tupac Inca Yupanqui* went to the Cañari province and in the way, when he conquered a place named Palta, he brought to Cozco and their warm valleys a tasty and pleasant fruit that they called *Palta*. Today, Cañari is part of Ecuador and it is known that *Yupanqui* conquered this province between 1450 and 1475 A.C. (de la Vega 1995).

From this perspective, it seems that the domestication process of avocado may have passed, at least, through four phases. The primary phase occurred with the avocado exploitation on the original forest vegetation when avocado was naturally occurring in the forests near the first human settlements. The secondary phase started when climate changed and the availability of wild stands was reduced and avocado cultivation began necessary to maintain it near people as a flavored food item. The tertiary phase started when the forest trees were transported from their natural habitats to more productive habitats and intentional cultivation and selection began. In this view, homegardens represent an intermediate land use system for the incorporation of trees in agricultural cropping systems and cultivation (Weirsum 2004) and they are an interesting example for the third phase and a prelude for the fourth phase: the cultivation of modern genetically modified tree crops.

Moreover, because the cultural diversity of the populations where avocado has been domesticated, it seems that more than one domestication took place (Clegg et al. 1993). These domestications occurred independently for alternative purposes and different necessities determined by the diverse cultures and climatic conditions, probably resulting in different breeds.

Evidence supporting that different cultures living in Mesoamerica in pre-Hispanic times had special interest in the avocado tree is the linguistic recognition of avocado by them. Example of the names that different cultures gave to avocado are the Huastec (uj), Maya, Tzental, Tzontil, and Chanabal (on), Chontal and Tzontzil (un), Choi (um), Quekchi (o), Pokomchi, Pokoman, Cakchiquel, Quiche,

Uspanteca, Aguacateca (oj) (Gama-Campillo and Gómez 1992), Otomi (nttzani), Aztec (ahuacatl), Zapotec (yasu, yashu, ishu, and isu), Mixe (cuchpa), Inca (palta) (Popenoe et al. 1997).

## Conclusions

The relationship between avocado and mankind has an ancient history, avocado was appreciated as a valuable food plant since pre-historic times. Archaeological remains provide evidence that avocado was consumed by humans since 8,000–7,000 B.C. (Smith 1966) and that the Neolithic farmers practiced a mixed exploitation of wild plants, showing a predominance for fruits (Betz 1999). Because of this, it seems reasonable that initial avocado exploitation could start by this time. There is also evidence that avocado cultivation could start when climate became variable and dryer around 4,500–2,000 B.C. (Buckler et al. 1998). According to this evidence it seems that in Mesoamerica, trees domestication started before annual crops, and avocado was one of these trees.

The first domesticates probably arose since the first human groups started using and consuming the avocado. Later the first Mesoamerican cultures as the Mokaya continued the domestication process and inherited its knowledge to other cultures as the Olmecs and Mayas. The Olmecs took avocado to Honduras and after them, other cultures as the Maya and Valdivia dispersed avocado in Central America and in northern South America, respectively. As avocado was a widespread and diverse species, before Spanish arrived; it seems that different domestications occurred independently for alternative purposes and different necessities determined by people and climatic conditions, resulting in much of the actual species diversity.

Avocado not only was appreciated as a food item by pre-Columbian people in Mesoamerica, it also had a religious and mythological meaning in some cultures, and also was used to pay tribute and with medicinal purposes.

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