

Chapter 11

Evolutionary Ethnobotanical Studies of Incipient Domestication of Plants in Mesoamerica

Alejandro Casas, José Blancas, Adriana Otero-Arnaiz, Jeniffer Cruse-Sanders, Rafael Lira, Aidé Avendaño, Fabiola Parra, Susana Guillén, Carmen J. Figueredo, Ignacio Torres, and Selene Rangel-Landa

Abstract Human cultures that occupied the area currently known as Mesoamerica developed a broad repertory of technologies for managing the biotic resources and ecosystems of the surrounding areas they lived. These technologies emerged from early experiences and had long time, enough for leading to the first forms of agriculture of the New World. Mesoamerica is actually recognized as one of the regions where agriculture and domestication of plants originated, with nearly 10,000 years

A. Casas, Ph.D. (✉) • F. Parra, Dra. • S. Guillén, Dr. • C.J. Figueredo
I. Torres • S. Rangel-Landa, M.Sc.

Instituto de Investigaciones en Ecosistemas y Sustentabilidad (IIES), Universidad Nacional Autónoma de México, Campus Morelia, Michoacán, Antigua Carretera a Pátzcuaro 8711, Col. San José de la Huerta, Morelia, Michoacán C.P. 58190, Mexico
e-mail: acasas@cieco.unam.mx; fabiolaparra@lamolina.edu.pe; sguillenro@conacyt.mx; itorresg@cieco.unam.mx; srangel@cieco.unam.mx

A. Otero-Arnaiz

Instituto Nacional de Ecología y Cambio Climático (INECC), Periférico Sur 5000, Col. Insurgentes Cuicuilco, Delegación Coyoacán, Distrito Federal 04530, Mexico

J. Cruse-Sanders

Atlanta Botanical Garden, 1345 Piedmont Avenue NE., Atlanta, GA 30309, USA

R. Lira, Ph.D.

Unidad de Biotecnología y Prototipos (UBIPRO), Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: rlira@unam.mx

A. Avendaño, Ph.D.

Salud Intercultural, Universidad Intercultural del Estado de Mexico, Libramiento Francisco Villa S/N, Centro, San Felipe del Progreso 50640, Estado de México, Mexico
e-mail: aaide3@hotmail.com

J. Blancas, Ph.D.

Centro de Investigación en Biodiversidad y Conservación (CIByC), Universidad Autónoma del Estado de Morelos, Av. Universidad No. 1001, Col. Chamilpa, Cuernavaca, Morelos P.C. 62209, Mexico
e-mail: jose.blancas@uaem.mx

of antiquity. This chapter summarizes ethnobotanical, ecological, and evolutionary information documented in different regions of Mexico, combining different research approaches in order to understand the human motives for managing plant resources, and the ecological and evolutionary consequences of management of plants and ecosystems. We therefore analyse those processes involving domestication as part of general design of nature according to human needs and desires, occurring at the levels of plant population of particular species, but also at the level of ecosystems and landscapes. We pay particular attention in the analysis of plant species that in the Mesoamerican area have wild and domesticated populations and maintain reproductive interactions. These interactions allow exploring practices and natural processes intervening in conforming populations in which divergence populations guided by natural and artificial selection and other evolutionary forces are occurring. Because natural processes continually weaken the human activities, the divergence is relatively slight and we have therefore called these processes incipient domestication. We analyse the cases of traditional greens called ‘quelites’ such as *Anoda cristata* and *Crotalaria pumila* in which people distinguish favourable and unfavourable morphs and practice artificial selection resulting in the abundance of the favourable morphs in areas more intensively managed. Similarly, some examples are analysed of trees (*Leucaena esculenta*, *Crescentia* spp. *Spondias purpurea*, *S. mombin*, and *Sideroxylon palmeri*), agaves (*Agave inaequidens* and *A. hookeri*), and columnar cacti (*Escontria chiotilla*, *Myrtillocactus schenckii*, *Pachycereus hollianus*, *Polaskia* spp., *Stenocereus* spp.). In the cases studied we analysed divergence in morphology, reproduction, population genetics, and germination patterns, among other features, between wild, silvicultural managed and cultivated populations. These case studies allow demonstrating that evolutionary divergence influenced by humans occurs not only under agriculture but also under silvicultural management and we hypothesize that domestication under silvicultural systems could have led to the origins of agriculture.

Different disciplines have generated relevant information for answering questions about when, where, and how agriculture and domestication originated. However, the answers about how and why these processes arose continue being motive of intense debate. With the information from our case studies we aspire to contribute elements of ongoing processes of domestication that could provide important examples about how processes could have happened in the past. In addition to their theoretical value, these cases may also contribute to establish important bases of policies for conserving the Mesoamerican biocultural heritage, as well as technological experiences that may be useful for the sustainable management of local resources and ecosystems.

Keywords Mesoamerica • Domestication • Ethnobotany • Incipient domestication • Sustainable management

Introduction

In this chapter we show a summarized panorama of our studies on incipient management and domestication in the Mesoamerican area of Mexico. Paul Kirchoff [1]

firstly used the term Mesoamerica to define a cultural region whose peoples share and shared in the past cultural elements such as consumption of maize tortillas as staple food, drinking of the fermented beverage ‘pulque’, among other dozens of aspects. Matos-Moctezuma [2] identified this region between the southern half of Mexico and the northwest of Costa Rica, but he recognized that it has been a dynamic territory with variable frontiers throughout history.

The Mesoamerican human cultures developed a vast repertory of technologies for managing biotic resources and ecosystems. It was one of the earliest experiences in the Americas and currently the region is recognized as one of the primary centres of origin of domestication of plants and agriculture of the world, with nearly 10,000 years of antiquity [3, 4]. Although there is an influence nearly 500 years old of human culture and management techniques introduced from the Old World, a high diversity of pre-Columbian cultural elements and technologies are still alive, mainly in the rural indigenous areas of the region. These elements make possible reconstructing scenarios of the Mesoamerican life in the past but, importantly, make possible the inclusion of them in designing the future life of the region. Our research group has conducted studies in different regions of the Mexican Mesoamerica, combining ethnobiological, ecological, and evolutionary approaches to understand motives and consequences of management (see Casas et al. in Chapter 8 of this book) of plants and ecosystems, and particularly the management that determines domestication. In this chapter we put particular attention on plant species that in Mesoamerica have wild and agricultural managed populations coexisting with forms of management considered as incipient. We have particular interest in understanding factors motivating invention, innovation, and adoption of new techniques and the socioecological consequences of such adoption. These are elementary questions to analyse the ‘why’ of the origins of agriculture. During the twentieth century and until the present, archaeology, radioactive isotopic dating, ethnography, ecology, molecular genetics, and ethnobiology among the most important scientific fields were able to generate important information for answering when, where, and how agriculture originated. However, the answers about the ‘why’ agriculture originated have remained fuzzy and controverted. Our research group considers that, because the processes of management and domestication are ongoing, their study may substantially contribute to answer this question and to understand what happened in the past. But in addition to looking for answers to questions of theoretical value, understanding such processes allow broadening our views about the Mesoamerican biocultural heritage for constructing sustainable management of natural resources and ecosystems in Mexico.

We look for analysing general patterns of the Mesoamerican culture of managing and domesticating plants. The region is exceptionally high in biocultural diversity; in a territory nearly 2 million of km² extent there is a great variety of natural ecosystems and landscapes constructed for thousands of years by the regional cultures [5–8]. It harbours a biological diversity represented by more than 25,000 plant species [9], nearly 1150 species of birds [10], and more than 500 species of mammals [11]. In addition, Mesoamerica harbours a high cultural diversity, with 58 indigenous ethnic groups which speak nearly 290 languages only in Mexico [12, 13]. The long history of interaction between traditional societies and the ecological

Table 11.1 Total number of plant species recorded in the floristic inventories of different regions of Mexico, and the total number of useful plant species recorded by ethnobotanical studies in those regions

Region	Total spp.	Useful spp.	%
Valle de Tehuacán	2621	1608	61.2
Sierra de Manantlán	2774	650	23.4
Selva Lacandona	1660	415	24.9
Los Tuxtlas	814	274	33.7
Tuxtepec	737	296	40.2
Uxpanapa	800	336	40.6
Península de Yucatán	2900	1000	23.4
Sian Ka'an	558	316	56.6
Montaña de Guerrero	800	430	53.8
Sierra Huichola	1652	532	32.2
México	30,000	11,700	39.0
	25,000	9750	39.0

The last column indicates the percentage of useful species in relation to the total flora recorded for each region. The bold number for Mexico are the estimated numbers of useful plant species that would be expected based on the average percentage (39 %) estimated in the sample of regions considered

biological diversity of their territories has modelled one of the most important bio-cultural legacies of the world [6, 7, 14, 15].

Caballero et al. [16] estimated that Mexican ethnoflora comprises between 5000 and 7000 plant species utilized by different cultures. However, in the last decade it has been published information about inventories that allow supposing that the cipher is higher. For instance, only in the Tehuacán Valley Casas et al. [17] and Lira et al. [18] recorded more than 1600 useful plant species which are nearly 54 % of the regional flora. A similar comparison in other regions of Mexico allows averaging 39 % of the total flora of a region as useful plant species (Table 11.1), which suggests that from a total of 25,000 [9] to 30,000 [19] plant species of México, in its territory may be expected the existence of between 10,000 and 12,000 useful plant species.

In the Tehuacán Valley nearly 40 % of useful species receive some form of management [6]; if this proportion is similar in other regions of Mexico we should expect 4000–4800 plant species under some management type in the Mexican territory. Unfortunately the information available about this topic is still insufficient for a confident estimation. For the moment, the inventory of managed plant species of the database of the Jardín Botánico, UNAM [16] identifies less than 1000 species. Ashworth et al. [20] identified nearly 400 species of edible plant species, including introduced plant species. Currently, the available information allows conservatory estimation of the existence of 500 species of cultivated plants, nearly 200 of them being native to Mexico. But the inventory of managed plants and management forms of plants in Mexico is yet to be constructed.

Diversity of Domestication Pathways

Domestication is a word derived from the Latin term ‘domus’ meaning ‘house’; to domesticate is a verb that may mean ‘bringing to the house’ ‘to make something part of the house’, or ‘to construct the house’. All these meanings lead to theoretical implications of the term. The first one is that making something part of the house implies adapt it to the context of the house. In other words, to modelling things according to the needs of people that construct the house. This is probably the most popular meaning of the term domestication: to adequate living beings according to human needs. This general premise practically means to modelling morphology, physiology, and behaviour of plants, animals, and other organisms, according to human needs, culture, customs, technologies, and even curious inventions. It is recognized that such a process is an evolutionary process that involves inheritance of characters that keeps the memory of changes in one generation to the following ones.

The first scientist that formalized theory about domestication was Charles Darwin in the first chapter of the *Origins of Species* [21], and then in the two volumes work “Variation of Animals and Plants under Domestication” [22]. This theory allowed connecting the practice of breeders with the explanation of selection and variation in nature. Therefore, Darwin used domestication as a model to analyse the causes of variation in plants and animals as divergence in lineages connected with common ancestors mainly caused by artificial selection and adaptation. This general thinking was the basis for building the great theory of natural selection and the origins of biological diversity that revolutionised the human thinking about nature.

The general premises of the theory of domestication developed by Darwin were generally simple. Artificial selection favours through some way a fraction of organisms composing a population disfavours others, and this mechanism throughout time determines divergence and variation. Throughout the twentieth century, with the developing of the evolutionary theories, the studies of domestication found an extraordinary context for explaining the origins and diffusion of the most important domestic plant and animal species. Studying the processes of domestication continued making contributions to the development of evolutionary theories, since they continued being good models for representing natural evolutionary processes. Nevertheless, the progress in the study of domestication was extraordinarily limited to no much more than 100 domesticated species and part of their wild relatives. This situation contrasts with the nearly 3000 plant species clearly recognized as domesticates existing in the world. In addition, it is to say that most of the cases studied were annual plants (the most economically important cereals and legumes) and some perennials, particularly those trees and vines propagated by vegetative means. The study of these cases determined a general view of the processes of domestication centred in artificial selection of successive generations of organisms. However, the mechanisms through which artificial selection operates, the influence of other evolutionary forces such as genetic drift, breeding system and gene flow

that are generally recognized as important evolutionary processes in nature, are important problems yet to be studied in depth. In addition, it is necessary to broaden the spectrum of life histories of domesticates (long-lived perennials, different breeding systems, different targets of artificial selection), as well as the consideration that in areas where the wild relatives and crops coexist the gene flow is particularly intense and people make decision to favour or to control such gene flow. And finally, in areas where wild relatives and crops coexist it is possible to find intermediate stages of domestication. This is what we have called incipient domestication, and its understanding has particular value for analysing the processes that originated domestication and agriculture. Studying these latter problems is particularly important in Mesoamerica, one of the areas where processes of domestication originated.

The other principal meaning of domestication ‘to construct the house’ leads to an important dimension of the study of domestication: the modelling of landscapes or territories where people live and reproduce their lives. The domestication of plants and animals has been discussed as the main factor favouring the settled life. It is clear that the origin of the first human villages and cities represented the transformation of the general systems where the village and the artificial ecosystems the people started to construct. These villages coexisted with natural ecosystems which were in turn managed to solve a number of problems associated to the settled life: hydraulic systems for controlling floods, barriers against strong wind, and barriers against soil erosion, among other aspects. Soon it was clear that these transformations occurred earlier than the origins of settled life and that currently the landscapes and territories are human constructions directed to domesticate systems (ecosystems, landscapes, socioecological systems). Some authors have started the study of this perspective of domestication, considering it as part of the general process of intentional humanization of the world. Theoretical principles and mechanisms of landscape domestication are different to those used for understanding the domestication of species or populations of a species (the Darwinian approach described above). However, it is important to explicitly establish that both types of processes of domestication influence to each other. In other words, domestication operating at individuals or population of a species level are influenced and in turn influence those processes of domestication occurring at ecosystem or landscape level. In this chapter we will illustrate our studies of domestication analysed from the Darwinian perspective and we will finally discuss the connection that these processes have with the general intention of domesticating territories and landscapes.

Several authors have proposed that agriculture and pastoralism were strategies adopted by humans as predominant way of life in order to decrease uncertainty in the availability of plant and animal resources necessary for reproducing their lives [23, 24]. However, for thousands of years and until the present the rural communities, together with agriculture and pastoralism continued practicing extraction of resources from natural forests (gathering, hunting, and fishing). Currently, numerous plant resources are under forms of management that are neither gathering nor agriculture, and have been considered under incipient management since these forms of interactions are generally less complex than agriculture [14, 25, 26].

As discussed more deeply in the chapters by Blancas et al. and Casas et al. (Chapters 10 and 8 in this book, respectively), among these practices we include the

tolerance, which occurs when people clear the forest and leave standing some species and particular phenotypes of those species; induction, which involves the propagation of particular species and/or favourable phenotypes in order to increase their availability; protection by removing competitors, protecting against herbivores, parasites, excessive shade or solar radiation, among other aspects. All these interactions are carried out in situ in the areas where the organisms originate. Other forms of management occur out of such context and are called ex situ management in areas prepared and managed by humans. People use to bring there plants that are transplanted or sexual or vegetative propagules that are planted. As we have discussed these general forms of management may be carried out with different levels of intensity which may determine an extraordinarily broad spectrum of expressions of management types. We started the study of how these different expressions of management involve domestication and how domestication influence such management types.

Through domestication, human beings manage genetic variations or genetic resources mainly through artificial selection, but also through other evolutionary forces such as breeding systems, gene flow, and genetic drift. The mechanisms and criteria guiding domestication are deeply linked to human culture; therefore, domestication is eminently a biocultural research problem. It is consequently relevant to document the diversity of life forms of the organisms that are under domestication, the diversity of attributes that are identified, valued and differentially preferred by people, as well as the diversity of mechanisms through which the varieties of phenotypes preferred are favoured.

Through domestication people maintain diversity, generates continually new varieties, and also continually incorporate new diversity providing from other sites. Therefore, in terms of management and conservation of genetic resources, such a premise allows visualizing that more than the preservation of one or other variety (which is of course important), it is more relevant the maintenance of the whole process: the ecological, human cultural, and technological mechanisms influencing the generation of new variation, but also the natural processes such as conservation of wild crop relatives and gene flow among them and crops.

Cases Studied: Quelites, the Traditional Greens

Herbaceous plants but also leaves and flowers of shrubby and arboreal species are edible greens called 'quilitl' in Náhuatl [27]. Quelites (the plural term) are important plant resources complementing the diet of rural people in Mexico. Several studies conducted by our research group have found that among the Mixtec of La Montaña de Guerrero, quelites may be nearly 12 % of the biomass conforming the annual food of households, whereas in the Tehuacán Valley these constitute on average 11 % and in the Tarahumara region the diet of the Rarámuri may be nearly 19 % composed by plants gathered in wild and weedy populations, mainly quelites [28]. Some of these species are under incipient management and artificial selection practices have been documented to occur on them. We have studied the cases of 'alaches' (*Anoda cristata*) and 'chipiles' (*Crotalaria pumila*), in La Montaña de

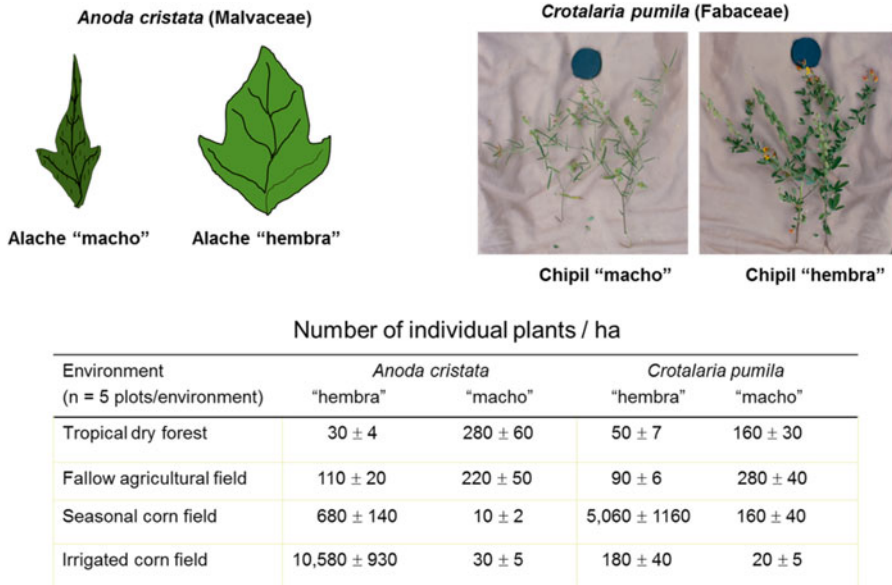


Fig. 11.1 *Anoda cristata* and *Crotalaria pumila*, species of quelites for which we analysed mechanisms of artificial selection in crop fields. People consume as *greens* the ‘hembra’ (‘female’) varieties, which are highly appreciated and have economic value in regional markets of La Montaña de Guerrero and the Tehuacán Valley. The table at the *bottom* of the figure indicates the number of plants per hectare estimated from 500 m² plots sampled in tropical dry forest and agricultural fields under different level of management intensity. It is notorious that the ‘hembra’ varieties of both species are scarce in environments under low management intensity whereas these are abundant in higher management intensity plots. The differences were highly significant (see Casas et al. [14])

Guerrero (Fig. 11.1). The details of these studies can be followed in Casas et al. [14, 26, 29]. In both species, people distinguish two phenotypes: the ‘macho’ (‘male’) and the ‘hembra’ (‘female’) varieties (Fig. 11.1). This classification is related to the quality of the plant resources not their sexuality; in fact, these are not the only species classified in this form. People of La Montaña de Guerrero also recognize the ‘macho’ and ‘hembra’ varieties of ‘epazote’ (*Chenopodium ambrosioides*), ‘laurel’ (*Litsea glaucescens*), ‘amole’ (*Phytolacca icosandra*), and ‘lengua de vaca’ (*Rumex* sp.), among others. The ‘macho’ varieties are generally plants with thinner, harder, and in some cases pubescent leaves, their flavour is generally bitter and their texture is fibrous. For the contrary, the ‘female’ varieties have wider, tender, glabrous leaves, with nicer flavour when prepared as food. People consume the ‘female’ varieties. They practice a differential let standing of female and male varieties during weeding, since both varieties of the two species grow in corn fields, favouring the ‘female’ varieties. After observing the selective weeding of these and other herbaceous species of quelites, we hypothesized that abundance of the ‘female’ and ‘male’ varieties should be different in active and in fallow agricultural fields. This hypothesis was established since we observed that in the forest the ‘male’ varieties

were more abundant than ‘female’ varieties. We finally sampled five plots of forest (tropical dry forest), other five in fallow agricultural fields, other five in active seasonal corn field, and other five in irrigated conditions agricultural fields. These four conditions were considered a gradient of intensity of human interventions, respectively, and we hypothesized that artificial selection favouring the ‘female’ varieties would be proportional to such management intensity. Our studies tested our hypothesis finding markedly higher abundance of female varieties in the more intensely cultivated areas and the ‘male’ varieties more abundant in the forest and in fallow agricultural fields (Fig. 11.1). This was a simple way to evaluate artificial selection occurring associated to practices that are not cultivation but simply differential tolerance of the presence of varieties. Our main doubt when we carried out that study was whether or not the differences among varieties were phenotypic plasticity. However, a recent study of quantitative genetics by Bernal-Ramírez [30] demonstrated that differences between ‘male’ and ‘female’ alaches have high heritability.

Recent studies by Blancas et al. [7] documented other species of quelites which are classified based on similar characteristics as those described above. In Coyomeapan, people recognize two varieties of *Brassica campestris*, one of them called “*colesh*” in Náhuatl with tender glabrous stems and leaves with nice flavour, the other called “*colesh teneztlí*” or “*cashtelanquilitl*” (meaning “goat *colesh*” in Náhuatl) with tomentous stems and leaves, asperous texture and bitter flavour. Plants called “*colesh*” are preferred and people collect and promote seeds of this variety, and tolerate it in parcels. Contrarily, plants called “*colesh teneztlí*” are removed during weeding of agricultural fields, and their seeds are never collected and sown. Other quelites are classified, used, and managed according to their colour. For instance, people of Coyomeapan recognize three varieties of *Amaranthus hybridus*: (a) white variety (light green inflorescence and leaves), (b) purple variety with red inflorescence and leaves with purple edges, and (c) spotted, with red inflorescence and leaves with purple spots. In general, people prefer the white variety which have tender leaves and better taste, but the aspect is also important, when boiled, the white variety produces green sauce (preferred), whereas the other varieties produce red sauce, which is associated with blood and not liked. It is similar in the case of *Porophyllum ruderale* about which people distinguish two varieties: (a) “white” variety with light green leaves and stems and (b) “purple” variety with leaves and stems with purple areas. The white variety is cultivated and available throughout the year whereas the purple variety is tolerated and available during the dry season.

Other attributes may also be significant in quelites perception, use, and management. For instance, Blancas et al. [7] found that in *Spathiphyllum cochlearispathum* (Liebm.) Engl. people recognize two varieties: (a) “*elotlxóchitl*” or “*oloxóchitl*”, which produces green inflorescences with nice flavour and easily cooked and (b) “*iztacxóchitl*”, which produces white inflorescences with bitter flavour, not consumed. People let standing and transplant the “*eloxochitl*” variety while removing the “*iztacxochitl*” variety. Similar hypotheses as tested in the studies of *Anoda cristata* and *Crotalaria pumila* could be examined in these latter cases in order to broaden information about mechanism and results of artificial selection in this group of plants.

Incipient Domestication of Trees

A number of tree species have been domesticated in Mexico. These include long-lived tropical species of the genera *Pouteria*, *Manilkara*, *Brosimum*, and *Persea*, other medium-sized species such as *Spondias* spp., *Theobroma cacao*, *Prunus capuli*, *Crataegus mexicana*, several species of *Leucaena*, *Crescentia* spp., among the most important. We studied the ‘guaje colorado’ tree *Leucaena esculenta* in La Montaña de Guerrero [14, 26, 31, 32], which allows illustrating mechanisms of domestication and research approaches different to those used for analysing artificial selection of quelites.

In La Montaña de Guerrero the Mixtec and Náhuatl peoples identify three varieties of *L. esculenta*: (a) the ‘guaje de vasca’, which is bitter and causes vomiting reactions to whom consume their seeds, (b) the ‘guaje amargo’, which has bitter flavour and causes indigestion, and (c) the ‘guaje dulce’ which is not bitter, and does not cause digestive disorders. The bitter flavour is conferred by secondary chemical compounds (among them mimosine) that constitute defence mechanisms against herbivory. In addition to flavour and digestedness, people practice artificial selection in favour of trees producing larger seeds and pods. Trees of *L. esculenta* are part of the tropical dry forests of the region and can also be found in homegardens, intensively cultivated because their seeds are highly valued for consumption and their commercialization is active. Together with these wild and cultivated populations, people manage in agroforestry systems those trees that were part of the vegetation they cleared before establishing agricultural plots. But such presence is preceded by artificial selection. Since trees compete with maize and other crops for space, people have to remove them from the area, at least partially. They let standing selectively those trees producing the better pods and trees.

Considering the information summarized above, we hypothesized that in agroforestry systems we should find a higher frequency of the good phenotypes (not bitter, with larger seeds and pods) than in the wild, but not necessarily those cultivated phenotypes predominating in homegardens, which, according to local people, require more water and can not survive in the wild. Since chemical attributes are combined with other quantitative characters (seed and pod size) in artificial selection, we tested our hypothesis by estimating the frequency of phenotypes in wild, agroforestry systems and homegardens. In particular, we were interested in comparing wild and agroforestry systems because populations in those area have an origin in common and we wanted to test the effect of artificial selection on these not cultivated populations. We used different statistical techniques for testing our hypothesis. Figure 11.2 summarizes our findings, which allowed demonstrating that the ‘good phenotypes’, which produce larger seeds and pods, and no bitter seeds (the more vulnerable phenotypes to bruchids attack are those producing lower amount of secondary compounds that make bitter the seeds of the most resistant varieties) were significantly more frequent. Population genetics studies by Zárate et al. [32] found significant structure between wild and managed populations, which can be explained because the populations cultivated in homegardens are markedly differ-

Leucaena esculenta subsp. *esculenta*

Average values of seed and pod characters of wild and silviculturally managed populations of *Leucaena esculenta* in La Montaña de Guerrero. Different letters indicate significant differences.

Character	Wild 1	Wild 2	Managed 1	Managed 2	P
Seed length (cm)	0.795±0.018 A	0.755±0.018 A	0.894±0.018 B	0.896±0.018 B	0.0000
Pod length (cm)	12.876±0.610 A	12.879±0.610 A	14.891±0.610 B	15.284±0.610 B	0.0062
Number of seeds per pod	12.385±0.524 A	12.680±0.524 A	12.213±0.524 A	14.416±0.524 B	0.0144
Number of predated seeds by bruchids	3.933±0.809 A	1.752±0.809 A	6.724±0.809 B	11.22±0.809 C	0.0000

Fig. 11.2 General aspect of seeds and pods typical wild, silviculturally managed, and cultivated trees of the ‘guaje colorado’ *Leucaena esculenta* in La Montaña de Guerrero, Central Mexico. The photography at the *right* shows a panorama of the continuous morphological variation of seeds and pods found in a single populations (in the case illustrated a silviculturally managed population). The table illustrates the measure of characters of seeds and pods from wild and silviculturally managed populations and the standard error provided by ANOVA tests. The capital letters in each character indicate significant differences estimated according to multiple range tests of Tukey MSD

ent than wild populations and those populations in agroforestry systems are under artificial selection reducing the number of trees and favouring some particular phenotypes.

Another species studied was the ‘tempesquistle’ (*Sideroxylon palmeri*), whose fruits are widely commercialized in the Tehuacán Valley and the city of Oaxaca [33]. Tempesquistle was identified among the archaeological remains in the Coxcatlán cave of the Tehuacán Valley by MacNesih [3] and Smith [34]. At present, tempesquistle is cultivated in the areas near Coxcatlán but their natural populations are located up in the mountains. We studied wild, silvicultural managed and cultivated populations of this species in Santa María Coyula. Wild populations are part of the riparian vegetation associated to tropical dry forests at elevations 1800 m. However, local people from Coyula let standing this and other species in the agroforestry systems of the neighbouring areas. Tempesquistle is a culturally important plant species. People appreciate to consume its fruits when immature for preparing an olive-like fruit that is consumed in a variety of dishes. We have documented that fruits produced by three trees of this species have an economic value comparable with that produced by one hectare of maize [33]. Therefore, people take care of the

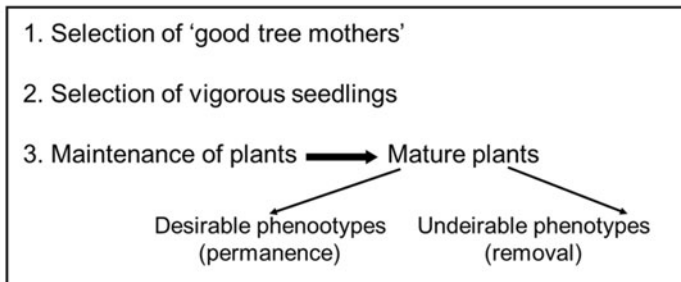
Sideroxylon palmeri

Fig. 11.3 The tempesquite *Sideroxylon palmeri*. *Left*: aspect of immature and mature fruits. *Right*: aspect of young plants propagated from seeds in pots. *Bottom*: general scheme of artificial selection practiced in favour of plants producing larger spherical fruits with lower amount of latex. In the first step, people select in wild or managed trees those mother trees with the desirable attributes. In a second step, people propagate seeds of the 'good mother trees', select the most vigorous young plants, and maintain the plants until their maturity. After their first production of fruit people decide to maintain or remove the planted trees

trees and let standing in their agroforestry systems, similarly as described above for *Leucaena esculenta* trees. They have a selective criterion to let these trees standing. Particularly they select trees producing larger spherical fruits with lower amount of latex. These criteria are also taken into account for cultivating trees in homegardens. However, in this case people practice artificial selection in two phases (Fig. 11.3). Firstly, they collect fruits and extract seeds from tree mothers producing larger fruits. They sow the seeds in pots or small seed beds in order to obtain seedlings. Then, they select the most vigorous seedlings and young plants for transplanting them in an appropriate place within the homegarden. After several years, when the young trees start producing fruits people make a second phase decision, let standing only those trees producing the best quality fruit. There is a selection of fruits in markets. Sellers and buyers make agreements about the price of tempesquite fruits and the larger fruits have generally higher price than the smaller ones. It is clear that people prefer larger fruits and they practice artificial selection when let standing in agroforestry systems and when sowing seeds and transplanting young plants in their homegardens. We recorded a similar form of managing seeds and young plants of *L. esculenta* in homegardens in La Montaña de Guerrero. It is clear that in both

cases the characteristics of the mother tree is not considered a guaranty that its descendants will have similar characteristics. In both cases breeding system is self-incompatible and segregation of characters does not allow a confident prediction of the attributes of the descendants. They select a good phenotype of mother tree, because that fact increases the probability to have good descendants, but they have to wait for some years to corroborate the result. The vigour of seedlings and young plants is an additional indicator of possible good phenotypes, but this is confirmed during the second phase of selection. Our morphometric studies revealed significant differences in fruit size of wild, agroforestry managed and cultivated trees in homegardens, being progressively of larger size, respectively [33].

We also studied the case of ‘pochotes’ *Ceiba aesculifolia* subsp. *parvifolia*. Seeds of this species were also found among the archaeological remains of the pre-historic records of plant resources used by ancient peoples of the Tehuacán Valley [3, 34]. Currently, ‘pochotes’ are plant resources highly valued by people of the region. They provide edible seeds and roots, and their capsules produce fibre that has been used for confectioning of textiles as well as for manufacturing adobes and other handcrafts. Seeds are very much appreciated, and their gathering and commercialization is at present one of the most important economic activity associated to forest products extraction [35–37]. Arellanes et al. [37] studied the vulnerability of plant resources in relation to their demand in markets and ecological information about their distribution and abundance throughout the region. These authors found that the information available indicates that this is one of the species with higher risk and especial care should be considered as part of the conservation policies promoted by the authorities of the Biosphere Reserve.

Avendaño et al. [35, 36] documented that people from Coxcatlán and Tilapa recognize several varieties of ‘pochote’ (Fig. 11.4). Local people prefer particularly seeds produced by the variety purple-reddish. Throughout time, in association to agroforestry systems, people has let standing this variety in areas recurrently used for establishing agricultural fields, followed by fallow periods. After probably hundreds or thousands of years, these areas have atypical abundance of this purple-reddish variety, which suggests that, as in the cases of the quelites and *L. esculenta*, the recurrent artificial selection in favour of this variety is the cause of its abundance.

Agave Inaequidens

Agaves are endemic to the Americas, with nearly 200 species [38] widely distributed in arid, semiarid, and temperate forests [39]. More than one hundred species have been important resources for indigenous cultures of Mesoamerica from the prehistory [40], as food, beverages, fibres, and medicine, among other uses [41]. Several species of *Agave* have been domesticated in the region but this process has been studied in only some few species. These are the cases of *Agave angustifolia* Haw., *A. fourcroydes* Lem., *A. rhodacantha* Trel., and *Agave tequilana* Weber

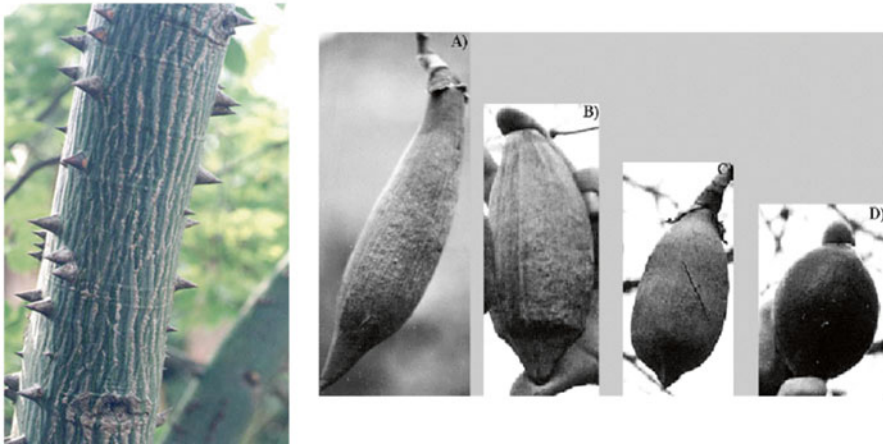
Ceiba aesculifolia subsp. *parviflora*

Fig. 11.4 *Ceiba aesculifolia* subsp. *parviflora*. General morphological aspects of the stem and the varieties expressed in fruit types

which produce fibre and mescal, studied by Colunga-GarcíaMarín et al. [42], Colunga-GarcíaMarín and Pat [43], Vargas-Ponce et al. [44, 45], Rodríguez-Garay et al. [46], and Zizumbo-Villareal et al. [47]. Also, *A. salmiana* Otto ex. Salm, *A. macroculemis* Tod., and *A. mapisaga* Trel., which are used for production of ‘pulque’ by Mora-López et al. [48]. Recently, aspects of domestication of *A. parryi* Engelm. and *A. parryi* var *huachucensis* were studied in southeast Arizona [49, 50]. In all these cases, the general trend found has been morphological and genetic divergence between wild and cultivated populations, domesticated plants having larger size, less and smaller spines, as well as lower genetic diversity than the wild ones, although some cultivated populations of *Agave angustifolia* were found having high genetic diversity because of the continual introduction of wild and cultivated varieties from different areas [45].

In central western Mexico, *Agave inaequidens* Koch and *Agave hookeri* Jacobi are widely used from ancient times for the extraction of fibres, sweet sap for preparing ‘pulque’, and as food [51, 52]. There is a gradient of management intensity for *A. inaequidens* in wild, in situ managed, and cultivated populations, whereas *A. hookeri* only is found as cultivated plant forming live fences. According to Gentry [51], this species is closely related with and probably derived from *A. inaequidens*. We have hypothesized that *A. hookeri* may be the extreme of the management intensity gradient as a domesticated-cultivated taxon. In order to test this hypothesis we documented patterns of morphological and genetic variation evaluating the degree of divergence according to the level of management intensity of *A. inaequidens* and *A. hookeri*.

We studied seven wild, two silviculturally in situ managed, and seven cultivated populations of *A. inaequidens*, as well as three cultivated populations of *A. hookeri*

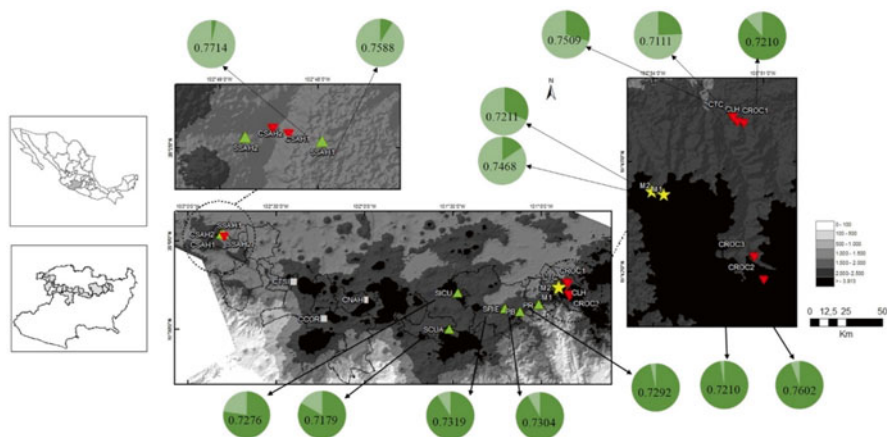


Fig. 11.5 Localization of the population of *Agave inaequidens* (green upward triangle) wild; (red downward triangle) cultivated; (star) managed y *A. hookeri* (square) studied in Central Occidental Mexico. Pie charts showing proportion of ancestry assigned to individuals of each population by Bayesian clustering analysis with STRUCTURE 2.3.4 (CITA) with $k=2$. The number inside the pie charts indicate the expected heterozygosity

(Fig. 11.5). We conducted ethnobotanical studies to document the management forms, mechanisms, and purposes of artificial selection and measured 25 morphological characters following criteria of previous studies on domestication of agaves [43], which were analysed through Discriminant Function Analysis (DFA). We in addition analysed genetic diversity, structure and gene flow of wild, silviculturally managed, and cultivated populations of *A. inaequidens* through nine microsatellite loci based on studies by Lindsay et al. [53] and Parker et al. [50]. We compared (H_E) among populations and conducted Bayesian group analyses to estimate the proportion of individuals in populations belonging to these groups.

A. inaequidens is called in the region ‘magüey bruto’ or ‘magüey alto’. The escapes or ‘quites’ are consumed as food, whereas the entire plants are used for the extraction of ‘sweet sap’ for preparing pulque and preparation of mescal. Mescal producers identify two to eight wild varieties of *A. inaequidens*, all of them based on differences in size (large or ‘magüey grande’ and small or ‘magüey chico’), colour (green or ‘verde’, light green or ‘cenizo’, and dark green or ‘negro’), form and size of leaves (wide or ‘magüey de hoja ancha’ and narrow or ‘magüey de hoja estrecha’), and according to their use (‘magüey bruto mezcal’ and ‘magüey bruto chapín’). For producing mescal, people collect all plants without distinction of varieties. Almost all mescal producers have plantations 15–20 years old (Fig. 11.6a), but only some few of them are ready to harvest, reason why the extraction of agaves from the wild is still important. Agaves in plantations generally are formed by seedlings collected in forest sites preferred to collect adult plants for mescal production and then transplanted (Fig. 11.6b). The producers also collect seeds from the largest and most vigorous plants; these are then sown in seed beds and the most vigorous

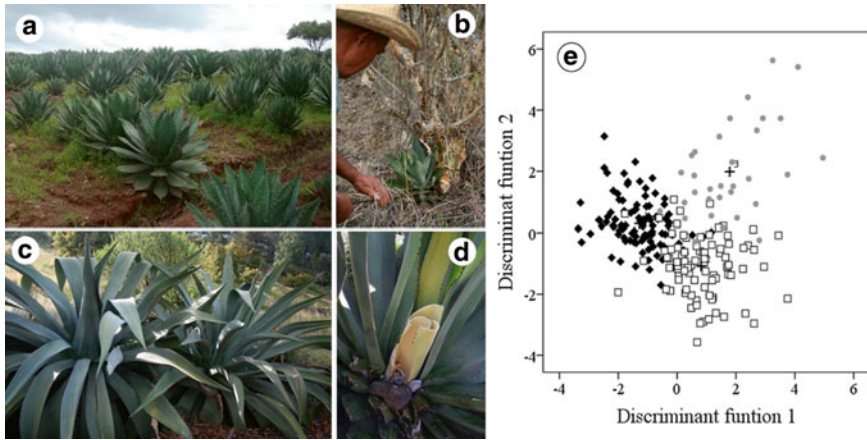


Fig. 11.6 (a) Cultivated population of *A. inaequidens*, (b) Collection of wild individuals for cultivation, (c) Individuals of *A. hookeri* in live fence, (d) Hollow in central cormo of *A. hookeri* to the collection of “agua miel”, (e) Classification of *Agave inaequidens* individual according type of management and *A. hookeri* individual using Discriminant Function Analysis (DFA) (filled diamond) wild; (square) cultivated (filled circle) *A. hookeri*, (plus) centroid group. The first discriminant function explains 58 % of variation and the second one 42 %, both being significant (DF1 Wilk’s $\lambda=0.190$, $p<0.001$; DF2 Wilk’s $\lambda=0.476$, $p<0.001$) (photos by Ignacio Torres)

seedlings are then transplanted to the plantation area. Vegetative propagation of *A. inaequidens* is inviable.

The main use of *A. hookeri* (Fig. 11.6c) is extraction of sap for preparing ‘pulque’ (Fig. 11.6d). After collected the sap, agaves of this species usually produce sprouts in the cormo, which are transplanted and maintained.

According to the DFA morphological differences are significant between wild and cultivated plants of *A. inaequidens* and these with respect *A. hookeri* (Fig. 11.6e). Most plants (88 %) were correctly classified according to their provenance. The main characters contributing to discrimination of groups are height and diameter of the plant, length and width of leaves, and size of the terminal spine. Plants of cultivated *A. inaequidens* are larger than wild plants, and plants of *A. hookeri* are larger than those of *A. inaequidens*.

A. inaequidens has relatively high levels of genetic diversity (H_E 0.711–0.771, Fig. 11.5), the highest recorded in this genus hitherto [54]. But no differences were identified in the levels of diversity among wild and managed populations ($F_{0.05,2}$; $p=0.200$). The Bayesian analysis identified $k=2$ most probable genetic groups, but the discontinuity is not associated to limitation of gene flow among wild and managed populations. It appears to be rather associated with the type of habitat, whereas the high gene flow appears to be related to the movement of pollen by bats and the movement of seeds by natural factors, and importantly associated to cultivation by mescal producers.

Our results suggest that the divergence among wild and cultivated populations of *A. inaequidens* can be appreciated through morphological features that are targets of

artificial selection, but no genetic structure can be identified through the neutral markers (microsatellites) used in the study. *A. hookeri* is clearly distinguished from *A. inaequidens* and the genetic relation between the two taxa is still under study.

Columnar Cacti

The system that we have studied with more detail is a group of seven species of columnar cacti (Fig. 11.7), which are plant resources of great economic and cultural importance in several regions of Mexico, particularly in the Tehuacán Valley and the Balsas River Basin. This group of species makes possible analysing the magnitude of divergence in a gradient of management intensity. We included in this analysis the ‘jotilla’ (*Escontria chiotilla*), which is not cultivated since it does not have vegetative propagation and after sowing seeds people should wait for decades before its first production of fruits, because of its slow growth. Other species like *Neobuxbaumia tetetzo* produce fruits of excellent flavour and are very appreciated by people, but these species have even slower growth than ‘jotilla’. The cultivation

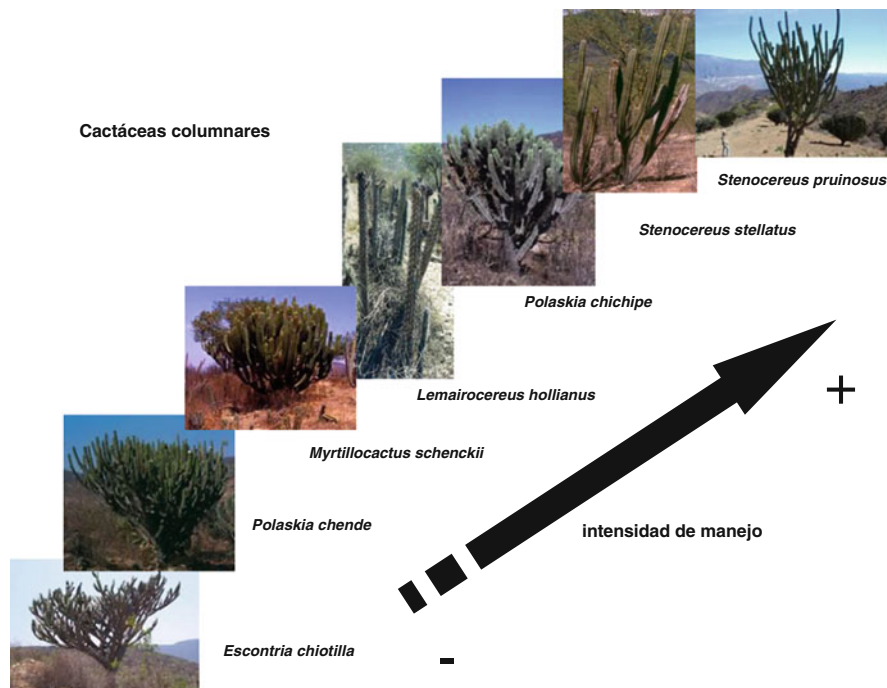


Fig. 11.7 Species of columnar cacti studied by our research team. We indicate the level of management intensity through the *ascendent arrow*, which was defined according to growth rate, viability of management associated to the possibility of vegetative propagation, and the intensity of artificial selection practiced by people

of these species is possible and actually their cultivation have been recently started for producing ornamental plants, but their cultivation for producing fruit is considered non-profitable activity. However, these species are managed in the agroforestry systems where people let standing selectively some particular plants, protecting or transplanting individuals from one site to other. But other species such as the ‘pitaya de mayo’ (*Stenocereus pruinosus*) or the ‘pitaya de agosto’ (*Stenocereus stellatus*) are intensively cultivated, coexisting with wild populations. These species are vegetatively propagated by planting their branches; this attribute and its fast growth stimulate people to carry out their cultivation. In these species the processes of artificial selection are also more intense than on species of slow growth [14]. With these species illustrating extreme states of management intensity, as well as others with intermediate states, it is possible to visualize the gradient of management intensity referred to above, which in these cacti depend on the viability of management, the growth rate, among other aspects.

We have hypothesized that populations silviculturally or in situ managed are more similar to those of the wild populations, but if the management is intense the diversification should be more pronounced (Fig. 11.8). Such hypothesis is useful to analyse diversification of morphology, as well as reproductive and population genetics parameters.

Ethnobotanical information is crucial for studying domestication processes because artificial selection is practiced by persons with culture, social organization, technology, and institutions. It is possible to talk to them which species are more valued, which aspects of these species they value, what are the intentions of artificial selection, which techniques are involved. For studying artificial selection is therefore important to document how people perceive that variation. In Fig. 11.9 we illustrate the perception of variation of columnar cacti species by the Mixtec. It is possible to identify the general classification of species and varieties [55]. The ‘*ndichicaya*’ (*Stenocereus stellatus*), for instance, is in turn classified into varieties according to particular attributes like colour, flavour, texture, and peel thickness, among other features (Fig. 11.10). All these characters are meaningful to people and it is possible to identify how meaningful are, what they take into account for selection, and how they carry out artificial selection. This information allows identifying what is pertinent to be evaluated to analyse the consequences of artificial selection in morphological aspects.

One of the main questions is to whether the patterns of variation in these characters allow to identify patterns of morphological divergence among wild and cultivated populations and how divergent these are. We have analysed such question in several species. Figure 11.11 shows multivariate analyses of morphological characters among wild (W), silviculturally managed (M), and cultivated (C). Individuals closer among themselves are morphologically more similar and vice versa. The Fig. 11.11 illustrates that in *Escontria chiotilla*, the least intensely managed studied the wild and managed plants have relatively lower differentiation than wild and managed individuals of *Stenocereus stellatus*, which is also more intensely managed. It

is possible to see that some wild and cultivated plants are similar among themselves. This is explainable because people continue introducing into cultivation wild plants in the managed systems, and also because in wild populations there is variation and part of such variation may include plants similar to those in cultivated areas. In fact, some of these plants are sources of material that is propagated in the managed systems. This information may be documented through interviews and corroborated through molecular markers [56].

We have used indexes of diversity and morphological differentiation that allow to integrate multivariate information. The differentiation index with values close to one would indicate higher differentiation and vice versa those closer to one. If our hypothesis is correct, we would expect higher differentiation between wild populations and those more intensely managed. Our results generally confirm this hypothesis as it can be seen in Table 11.2.

Studies of population genetics have generally documented higher genetic diversity in wild than in cultivated populations. This is because the wild relatives of cultivated plants have evolved for thousands and millions of years whereas domestication is a process of some few thousands of years. However in some species the managed and cultivated populations may be reservoirs of high genetic diversity, even higher than in some wild populations. This may be explained in part because people continually introduce plant materials from wild populations into cultivated areas; also, because the genetic interaction through pollen and seeds is likely maintained in areas where wild and cultivated populations coexist. And also, because people continually renew plants composing their managed areas, including plant material from other villages or regions. In other words, managed areas may be reservoirs of plant materials of highly diverse origin. Such traditional managed areas are, therefore, particularly important to be considered in programmes for in situ conservation of genetic resources.

We also hypothesized that divergence in reproductive patterns and germination of wild and managed populations would be more pronounced in populations and species under higher management intensity, and we have found patterns consistent with this hypothesis. Most of the species that we have studied are self-compatible, but in species like *Polaskia chichi* and *Myrtillocactus schenckii* in which we have recorded low frequency of self-pollination in the wild, this breeding system is markedly more frequent in cultivated populations. This is possibly an effect of artificial selection in favour of more productive plants. Self-pollinated plants may produce fruit even when the populations of flower visitors decrease for environmental or human causes.

The species of the genus *Stenocereus* that we have studied are all self-incompatible, pollinated by bats. In theory, wild and cultivated populations of *Stenocereus* may interchange pollen even at long distance since bats may fly until 100 km in one night. However, we have identified that wild and cultivated populations separated by some few kilometres are visited by different species of bats. Arias C6yotl et al. [57] documented that homegardens of cultivated populations of *Stenocereus* have much higher density of flowers than wild populations and are

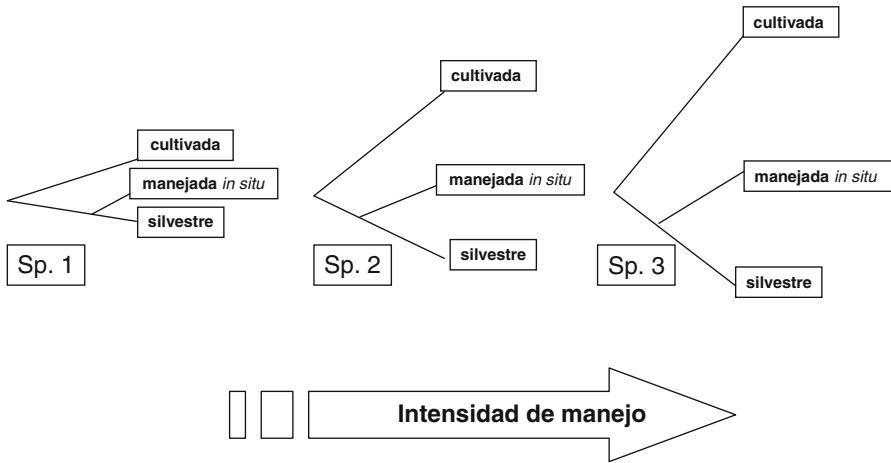


Fig. 11.8 Divergence in morphological, physiological, and genetic aspects expected between wild, silviculturally managed (in situ managed), and cultivated populations within and among species within a gradient of management intensity

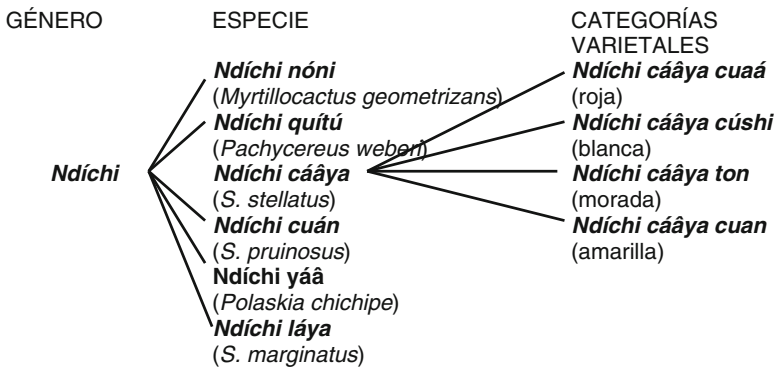


Fig. 11.9 Example of traditional perception of variation of columnar cacti. Mixtec classification of some columnar cacti species. All species of the group are classified through the term *ndíchi* which makes reference to the edible fruit of cacti. The name *ndíchi* is accompanied with an adjective indicating particular characteristics of each species. The varieties are named using particular attributes, in the first instance generally the colour of the pulp, then the size and/or the soar or sweet flavour

therefore more abundant sources of nectar and pollen. These authors found that cultivated populations are significantly more visited by *Leptonycteris yerbabuenae* whereas the wild populations are visited more frequently by *Choeronycteris Mexicana*, probably because one species is more tolerant to disturbance than the other or probably because of competence, but these are still hypotheses to be tested. A similar pattern was found in *Myrtillocactus schenckii*, in which the cultivated populations also offer a much higher number of flowers than wild populations. Flowers of wild populations are much more visited by the small stingless bees

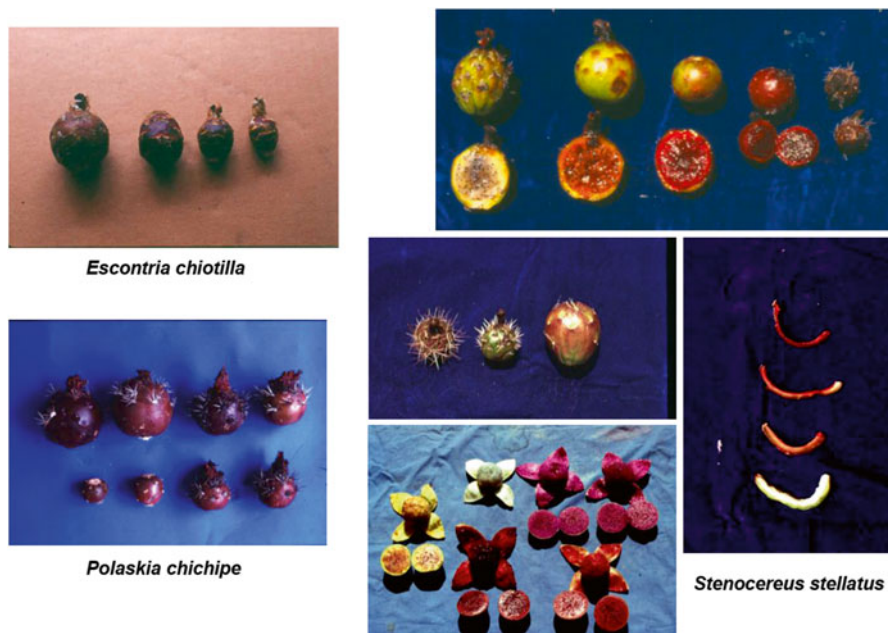


Fig. 11.10 Panorama of the morphological variation in some features significant for people managing *Escontria chiotilla*, *Polaskia chichipe*, and *Stenocereus stellatus*

Plebeia, whereas the cultivated populations are much more visited by the carpenter bee *Xylocopa mexicanorum* (Fig. 11.12). The differences could be due to differential capacity to resist disturbance but also because of competence. We also should comment that in *Polaskia* and *Myrtillocactus* we have recorded differences in the flowering peaks. And all these differences may contribute partially to maintain the divergences of wild and cultivated populations, although the main force maintaining the divergence is artificial selection.

Studying patterns of seed germination and seedling survival, Guillen et al. [58–60] also confirmed that divergence in seed germination and seedling survival and growth are more pronounced in species under higher management intensity. However, the conditions of humidity and shade in which such differences can be observed vary among the species analysed, which has been attributed to the particular adaptations at species level. The most intensely managed species are those with more successful vegetative reproduction, and therefore, the seed germination and seedling survival are not aspects directly submitted to artificial selection. However, the authors have found that artificial selection favouring larger fruits indirectly favours larger seeds that produce more vigorous seedlings able to survive and grow under conditions of shade and water availability, but that are more vulnerable to xeric conditions typical of the wild populations. This is another factor that allows explaining the differentiation maintaining between wild and cultivated populations (Fig. 11.13).

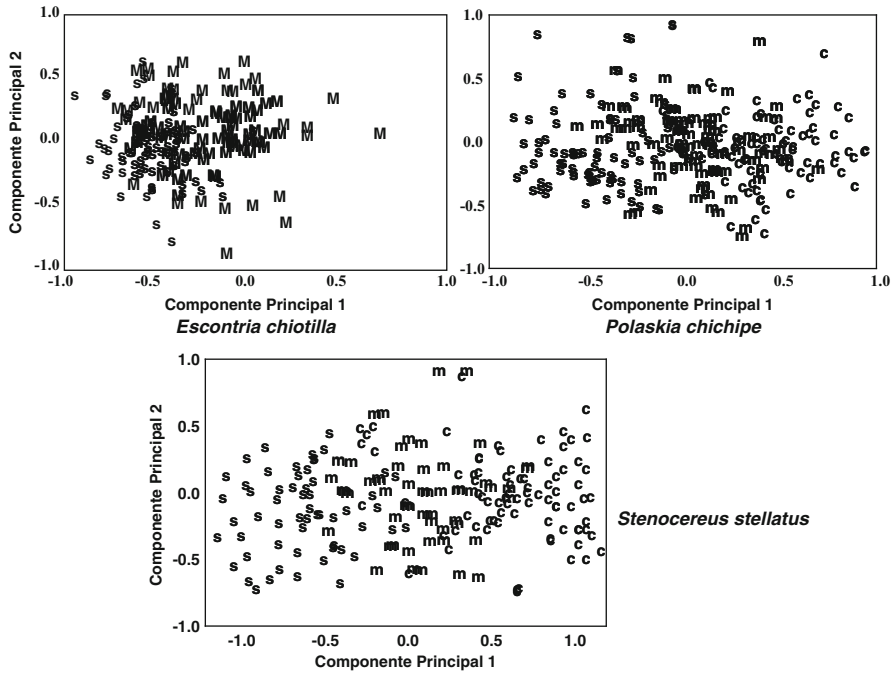


Fig. 11.11 Principal component analyses of the morphology of columnar cacti individuals from wild (s), in situ or silviculturally managed (m) and cultivated (c) populations. Each letter indicates one individual plant, its position in the plot depends on the general morphology (considering 15–23 morphological characters), individuals closer among themselves are more similar among themselves, and vice versa. Notice that the degree of differentiation of wild, silviculturally managed, and cultivated individuals is more pronounced in the species more intensely managed (*Stenocereus stellatus*)

Mesoamerican Patterns of Plant Domestication? Research Perspectives

Recently, we compared trends and mechanisms of domestication of Mesoamerica with those from Brazilian cultures [61]. Also, we have attempted to compare Mesoamerican with Andean patterns. But it appears to be premature to conclude about the features of regional patterns since we have only partial views of what appears to be a wide world of human cultural criteria and mechanisms of artificial selection. Also, because we have not studied with similar methodological approaches these aspects in the different regions mentioned.

It is possible to say that criteria of artificial selection or potential artificial selection can be detected in practices of gathering wild products. People identify varieties and their preferable attributes in wild populations. It is also possible to say that artificial selection is not only associated to cultivation but also to silvicultural management. Practices of in situ management (tolerance, enhancing, and protection)

Table 11.2 Morphological differentiation among wild, silviculturally managed, and cultivated populations of columnnar cacti

Especie	diferenciación entre poblaciones silvestres y silvícolas	diferenciación entre poblaciones silvestres y cultivadas
	<i>Polaskia chende</i>	0.009
<i>Escontria chionilla</i>	0.011	–
<i>Myrtillocactus schenckii</i>	0.069	0.110
<i>Polaskia chichi</i>	0.193	0.353
<i>Stenocereus stellatus</i>	0.251	0.379
<i>Stenocereus pruinosus</i>	?	?

The direction of the arrows indicates the direction of management intensity among species (*vertical arrow*) and among populations within each species (*horizontal arrow*)

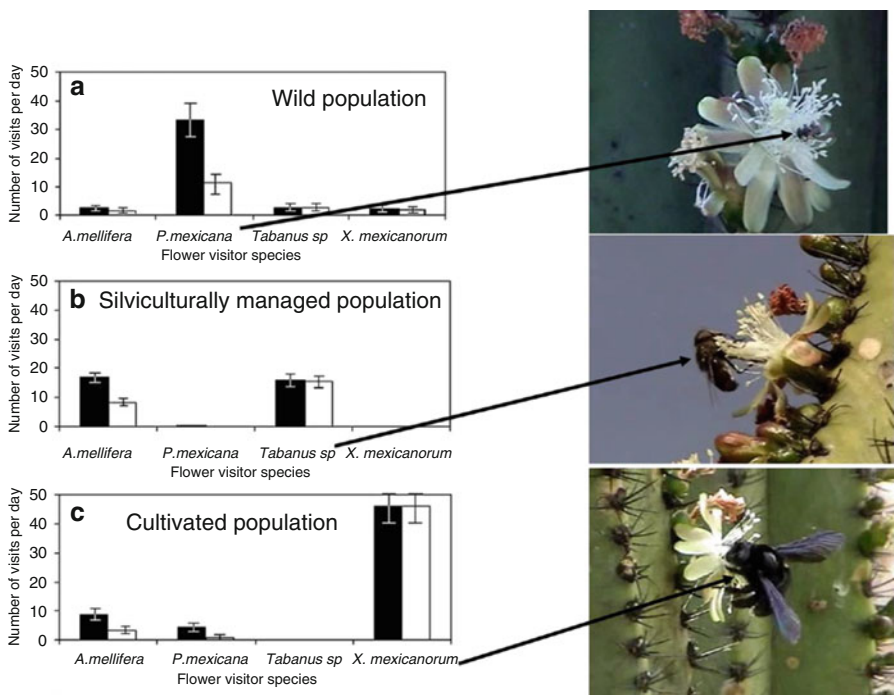


Fig. 11.12 General aspect of differential frequency visits to flowers of *Myrtillocactus schenckii* by meliponini bees (*Plebeia mexicana*) in wild populations, *Tabanus sp.* in silviculturally managed populations, and *Xylocopa mexicanorum* in cultivated populations. The differences in visit rates allows explaining partially the maintenance of morphological and genetic divergences among wild and managed populations, nut causes of the differential visits to populations are not studied yet

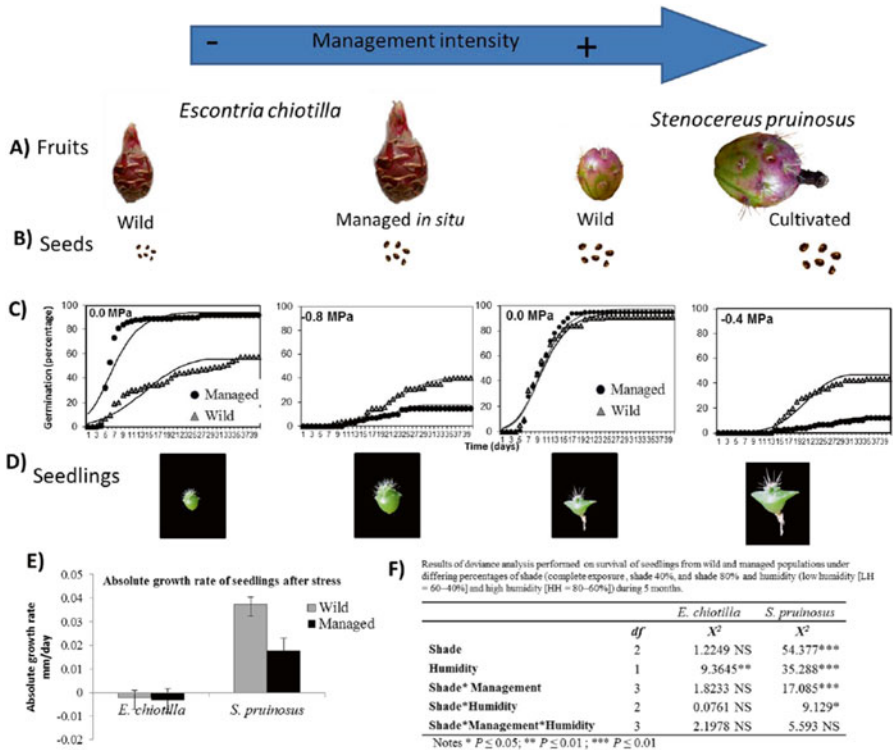


Fig. 11.13 Differences found in fruit size, seed size, seed germination capacity, and seedling survival and growth of two species of columnar cacti (*Escontria chiotilla* at the left, *Stenocereus stellatus* at the right). Our study comprised a continuum of six species in a gradient of artificial selection (indicated by the direction of the arrow at the top of the figure), but in this image we illustrate two of the extremes. During the process of domestication people selected directly in favour of larger fruits (a), which produce in turn larger seeds (b) that are more vulnerable to hydric stress than wild seeds (c), and produce larger seedlings (d) that are more susceptible in xeric conditions than wild seedlings (lower growth rate (e)) and significantly lower survival (f)

and ex situ management (seed sowing and planting of vegetative parts or entire plants) are common silvicultural practices associated to agroforestry systems in Mesoamerica, as well as in the Andean, the Amazonian, and semiarid regions of South America. All these silvicultural practices involve artificial selection favouring or disfavouring presence of particular species (differential species composition), as well as particular phenotypes. This artificial selection has had consequences on morphology, reproduction, and population genetics and, therefore, are expressions of domestication associated to silvicultural management.

Artificial selection may involve let standing and removal of plant elements, as well as selection of particular sexual and asexual propagules, and the process may be different according to the nature of the reproductive systems of plants, as well as their life cycle length.

Our studies are still a small window of the great variety of mechanisms of domestication of plants that potentially can be found in the field. Documenting and understanding such variation would make stronger the explanation of motives and mechanisms through which domestication and agriculture originated.

Ethnobotanists have widely documented forms of using plant resources by a number of human cultures throughout the world. But it is time to emphasize more the documentation and inventorying of management forms. We currently know and understand relatively few aspects about management and domestication and should direct higher efforts to document these aspects.

In addition to the socioecological complex processes motivating management and domestication, ethnobotanists have to document the consequences of management at population level. The morphometric, physiological, reproductive, and genetic studies are good tools to analyse the divergences among wild and managed populations. New tools are continually developed in evolutionary studies and these are particularly helpful for understanding domestication.

At present, evolutionary studies have the challenge of understanding the connection of adaptive features with the genetics of populations. The synthesis of quantitative genetics and molecular markers is developing new sources of tools and evidence that will make possible this type of holistic understanding. Similarly, phylogeography is nowadays an extraordinary helpful tool for analysing centres of origin and diffusion of domesticates and the experience of domesticating. Holistic approaches integrating phylogeography and archaeological research have demonstrated to be effective to understand these processes. The connections between the North-eastern USA, Mesoamerican, the Andean, and Amazonian experiences of domestication are still research problems that can be analysed through such integral research approach. Similarly, these 'main centres' or domestication can be explored at a finer scale. We have hypothesized for instance, that the Mesoamerican centre of domestication may be in reality a complex net of micro-centres that deserves to be analysed more deeply.

Landscapes are human constructions and expressions of domestication of ecosystems and environments. We have analysed how wild populations of particular species are connected with the domesticated populations, and how actions at landscape level may have consequences on domestication of such particular species. Also, we have identified that agroforestry systems are real laboratories of domestication of both landscape and particular plant species. The relation between forest management, agroforestry systems, silvicultural management, and agricultural systems are all aspects that should be more deeply understood from an integral perspective. Such a perspective may define a route for an integral analysis of domestication of landscape and the Darwinian approaches of the study of domestication processes.

Sustainable management of resources and ecosystems is one of the main challenges for science at society. Thousands of years of human experience are synthesized in the current ongoing processes of domestication. Therefore, the construction of future perspectives should recognize the value of these historical processes to construct innovation on such important bases.

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