Ethnobiology

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Ethnobotany of Mexico

Interactions of People and Plants in Mesoamerica

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Preface

Ethnobotany is a multi-, inter-, and transdisciplinary research field concerned with the study of interactions between people and plants throughout time and different cultural and ecological contexts. Such apparently simple concept involves a number of questions related with complex processes that require a broad spectrum of methods to be understood. Also, the solution of questions and hypotheses of such processes demands the participation of scientists and specialists in biology, agronomy, and anthropology, among other disciplines, and, particularly importantly, local people sharing their knowledge. Ethnobotany may be a science documenting what people know and do, but also it may be part of an interacting dialogue contributing to problem solutions and protecting intellectual and material property rights.

Ethnobotany has evolved from descriptive inventories of useful plants to the understanding of processes of domestication, the socio-ecological bases of sustainable management, as well as conservation and recovering of species and geographic areas. It has transited from questions about what species are used and how these are used to examine questions about why some plant resources are particularly important, how and why these are domesticated, as well as how and why humans have impacted their evolution and evolution of landscapes those plant species occur.

Sources of information feeding ethnobotany cover archaeological records, ethnographic approaches about the role of plants among human groups, molecular ecology, and evolution. Qualitative and quantitative approaches, descriptive, observational as well as experimenting and hypothesis-testing approaches are all important for constructing the emergent science field of ethnobotany. Dialogue and participation involved in transdisciplinary approaches are also crucial in validation and social construction of ethnobotanical knowledge.

The Mesoamerican and Aridamerican regions of Mexico are highly rich in biological and human cultural elements, which have been a great source of ethnobotanical knowledge and therefore a primary setting of ethnobotany's arising as empirical practice and evolution as modern scientific approach. We are therefore conscious that editing a book on Mexican ethnobotany is an ambitious task. It would require for sure several volumes and reflections along with the participation of numerous other scholars. This book, however, may be a first modest step of such a necessary ambitious project. It is an attempt of summarizing a general panorama of the history and current research perspectives and challenges of ethnobotany in Mexico. Additionally, it is a tribute to the work of different generations of ethnobotanists and an attempt to design a future perspective of this research field.

Certainly this compilation is incomplete, but surely it would inspire other colleagues to complement the panorama of the interactions between Mexican people and plants. And, more importantly, this work may contribute to enhance the design of new research for facing the contemporary problems, particularly the construction of sustainability science based on both, local and modern scientific knowledge.

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Chapter 1
Mexican Ethnobotany: Interactions of People and Plants in Mesoamerica

Alejandro Casas, José Blancas, and Rafael Lira

Abstract Ethnobotany is a research aimed at understanding what people know about plants, how plants form part of their systems of beliefs and conceptions of the world, and how humans make use and manage plants for reproducing their social and cultural life. This chapter shows a general panorama of the historical use of ethnobotany in Mexico from pre-Columbian times to the modern arising of ethnobotany as a research field, as well as the main contemporary methodological approaches and challenges of researchers working on Mexican ethnobotany. Such panorama conforms an introductory context for discussing the importance and limits of this book and a general description of the contributions of the each chapter that forms part of the text. We then discuss a general perspective of the Mexican ethnobotany in order to make stronger an "after description step" of this research field, recognizing the importance of descriptive methods but the need of emphasizing the analytical contribution of ethnobotany on research questions connected with research fields like anthropology, archaeology, ecology, and evolutionary biology. All these are research areas requiring support from both quantitative and qualitative ethnobotanical approaches in order to analyse social and anthropological problems such as the role of natural resources in human cultures, peoples' cosmovision, and their social organization and technology for interacting with ecosystems. Also, ethnobotany is necessary to ecology for studying important problems like the human

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influence on distribution and abundance of the flora of the world and the historical configuration of ecosystems. In addition, ethnobotany is crucial for understanding the past and ongoing processes of domestication in order to understand factors influencing the origins of agriculture. Ethnobotany is crucial for understanding evolutionary ecological processes influencing divergence between wild and managed populations of plants and perspectives of management of plant genetic resources. And finally, we discuss the general importance of ethnobotany as a bridge for building social–ecological views and trans-disciplinary approaches for constructing sustainability science. Ethnobotany is a promising research field for reinforcing the human understanding of nature and society, but also for solving practical problems in the context of the world's environmental crisis associated to global change.

Keywords Archaeobotany • Domestication • Ethnobotany • Mexican Mesoamerica • Plant management • Sustainability science

Introduction

Ethnobotany is a research field that looks for documenting and understanding what people know about plants, how plants form part of their systems of beliefs, explanations and conceptions of the world, and how humans make use and manage plants, as well as the social purposes related with such interactions [1]. Aspiring to synthesise the Mexican ethnobotany is an ambitious task, because of the vast human cultural and plant diversities, as well as the long history of their interactions occurring on its territory. Also, because of the high number of ethnobotanical studies carried out by numerous scholars, Mexico is in fact the setting of a high biodiversity, including one of the richest floras of the World [2–5] and one of the areas with more human cultures [6–8] and biocultural diversity of the Earth [9–12]. All these factors have propitiated that the territory of this country has been subject to numerous ethnobotanical studies, including some of the earliest researches in the modern step of the history of ethnobotany as scientific discipline, among them were those by Charles Christopher Parry in 1871. And, probably more importantly, Edward Palmer, who came to Mexico in Parry's expedition and then returned several times collecting botanical and ethnological information in the states of Coahuila, Durango, Tamaulipas, and San Luis Potosí [13, 14].

The history of interchange of views, knowledge, and experiences of humans about using and managing plants is as ancient as the experience of using plants for survival. It was probably a crucial way to survive and, therefore, ethnobotany and ethnozoology are probably among the most ancient empirical sciences developed by humans. The modern ethnobotany in Mexico is nearly one century old, and it is a relatively new scientific field. However, it is representative of an old interest and practice carried out by the human groups that populated the Mexican territory during pre-Columbian times from prehistory to the great Mesoamerican civilizations.

The early Mexican indigenous groups did not leave written records of their knowledge, but it is possible to make inferences about the importance of plant resources in their life through other type of information, archaeobotanical records being particularly important [15]. A number of plant remains were and continue being recorded by archaeological research, including studies of prehistory and more recent pre-Columbian times. In some archaeological sites like the Tehuacán Valley [16, 17] and Guilá Naquitz [18, 19], the archaeobotanical data provided information about use and management of plants testifying the long experience of human Mexican cultures in domesticating plants and starting agricultural processes, among the most ancient agricultural practices of the New World [15, 20]. Some of these studies revealed the most complete records of the first domesticated plants that Mesoamerica provided to the world, such as maize, beans, squashes, chili peppers, amaranth, chía, cocoa, cotton, among others [20].

The first written records of ethnobotanical studies of the world can be found among the most ancient writing of the Assyrian and Egyptian manuscripts art and artefacts [21, 22]. In Mexico, it is possible to find early records in pre-Columbian codices, but these are rather scarce since most of them were burned. The written records include the complex pictography started by the Olmeca, perfected by the Maya, Mixtec, and continued by the Nahua people [23–25]. These testimonies allowed reconstructing a clear idea about the importance of plant resources for the pre-Columbian civilizations. Unfortunately, there are relatively few codices since the Catholic Church ordered their destruction, whereas the abundant steles ornamenting the Mesoamerican temples were destructed during the Conquest and then looted by robbers of pre-Hispanic heritage. But the few information that remained out of these catastrophes shows a small sample of the great botanical knowledge developed by the regional cultures of Mexico. The Mesoamerican codices have valuable information about the broad spectrum of plant resources used, the life forms, ecological interactions, active principles, cultural meaning, forms of preparation and administration, amounts of products that were tribute to the dominant cultures which reflect their cultural and economic value, zones of extraction and production, commercial and interchange routes [24].

The earliest chronicles of the Conquest and the Spanish Colonial period, as well as the researches on the New Spain period documented, systematized, and interpreted the use of numerous plant species. Fray Bernardino de Sahagún in his General History of the things of the New Spain [25] described numerous plant species and varieties with particular uses for different purposes in the daily life and rituals. This is an extraordinary representation of the Aztec customs just before the arrival of the Europeans to Mexico [26]. The friar Fray Bernardino de Sahagún translated from Náhuatl (the Aztec language) into Spanish the Florentino Codex [25]. Sahagúns' work is one of the most outstanding ethnographic documents of pre-Columbian Mexico, since it provides information about Mexican indigenous life during the fifteenth and sixteenth centuries, just before the arrival of the Spanish conquerors. Also important were different chronicles of the conquest, which described the existence of botanical gardens and zoos in Mexico Tenochtitlan, as well as in other cities of the pre-Columbian Mesoamerica [25, 27], in a time when these living collections of plants and animals were not still established in Europe. Another outstanding work is the De la Cruz and Badiano Codex, written by the Náhuatl physician Martín de la Cruz and translated into Latin by Juan Badiano [28]. The *Libellus de medicinalibus indorum herbis*, the real title of the De la Cruz-Badiano Codex [28], mentions nearly 230 plant species used as remedies in combination with other mineral and animal components. The other crucial document of this epoch is the illustrated manuscript "Historia natural de la Nueva España" ("Natural history of the New Spain"), elaborated by Francisco Hernández de Toledo [29], the proto-physician of the king Phillip the Second of Spain. Hernández de Toledo participated in an expedition between 1571 and 1576 and compiled monumental information about more than 3000 plant species and nearly 500 animal species, among them 230 species of birds. The Francisco Hernández work [29] is the most important compendium of Náhuatl medicine and information on natural and cultural history of Mexico. Numerous species described included references about their medicinal properties and other uses practiced by indigenous people and that were recorded during the expedition. Unfortunately, the original manuscript and much of the unique information it contained were lost in the seventeenth century, when the library of the Escorial castle caught fire. All these classic works continue being important references for all scholars studying knowledge, practices, and beliefs of the Mexican cultures on plants.

During the sixteenth and seventeenth centuries, numerous manuscripts describing and frequently illustrating the indigenous and mestizo knowledge about plant use were produced, and all of them deserve special attention for the task of writing the history of Mexican knowledge of plants. Particularly important are the Relaciones Geográficas del Siglo XVI (Geographic Relations of the sixteenth century) [30] and the translation into Spanish of the "Cuatro Libros de la Naturaleza y Virtude de las Plantas y Animales que están reunidos en el uso de Medicina en la Nueva España y el metodo, corrección, y preparación, que para administrarlas se requiere con lo que el Doctor Francisco Hernandez escribió en Lengua Latina" ("Four books about nature and virtue of plants and animals compiled on the use of Medicine in the New Spain, as well as the method, correction, and preparation for prescription according to what the Doctor Francisco Hernández wrote in Latin") by Francisco Ximénez de Huaxtepec [31]. This is a medicinal summary of information originally recorded by Francisco Hernández, then recovered by the Physician of Phillip the II, Recco (who saved an important part of the original information of Hernández de Toledo), with additional notes and experiences by Francisco Ximénez himself. This work was published in Mexico in 1615 [31]. In the eighteenth century, the number of works describing the Mexican flora and fauna decreased. But it was the time when Carolus Linnaeus published his classic works classifying nature [32, 33], who included in his studies numerous species of plants and animals from Mexico.

During the nineteenth century, Mexico was involved in several wars and steps of constructing a Republic. However, some scientific activities were relevant for maintaining increasing botanical and ethnobotanical information of Mexico. Particular enormous value have the studies and sanitary campaigns by Dr. Balmis [34], the expeditions by José M. Mociño, Martin Sessé, and other naturalists, who participated in the Royal Botanical Expedition of the New Spain between 1787 and 1803 [35] and those carried out by Alexander Von Humboldt and Aimé Bonpland [36] by the end of the eighteenth and early nineteenth centuries, mostly based on the indigenous medicine and local botanical knowledge. Mexico became Independent from Spain and lost nearly one half of its territory in a war with the US. In this period of violence, the Mexican science had generally poor advances, particularly ethnobotany, since the indigenous knowledge was considered reminiscence of an undesirable past hindering the advances of the development as considered by the both conservative and liberal sectors in the context of constructing a dream of incipient modernity.

The modern concept and practice of ethnobotany arose by the end of the nineteenth century by the influence of John William Harshberger and Edward Palmer [13, 14], whose studies in Mexico continued until the beginning of the twentieth century. After the Mexican Revolution (1910–1917), the construction of new research institutions re-started their activities, among them was the National University of Mexico. By the 1940s and 1950s, it was particularly relevant that the seminal compilation of information on names, distribution, and uses were recorded by Maximimo Martínez, a primary and secondary school teacher. By 1914 and until 1929, he became helper at the Museo Nacional de Historia Natural, and later on he was the Director of Biological Studies of the Museum, particularly in charge of the Botanical Section. Maximino Martínez was a pioneer of the modern ethnobotanical studies in Mexico, publishing in 1923 the “Catálogo alfabético de nombres vulgares y científicos de plantas que existen en México” (“Alphabetically ordered catalogue of scientific and popular names of plants of Mexico”) [37]. Then, he published the “Las plantas útiles de la República Mexicana” (“The useful plants of the Mexican Republic”) in 1928 [38] and “Las Plantas Medicinales de México” (“The medicinal plants of Mexico”) in 1933 [39]. During the 1940s, he taught botany in the Instituto Politécnico Nacional and was one of the main founders of the Botanical Society of Mexico. In 1944, he was professor at the National Autonomous University of Mexico at the Institute of Biology and published a more elaborated catalogue of plant names and uses [37]. It is also important to mention that in this period some anthropologists in Mexico started to consider the need of ethnobiological studies for a deeper comprehension of ethnographic studies. This is, for instance, the case of Manuel Maldonado Koerdell, who in 1940 published some of the earlier Mexican anthropological premises about ethnobiology [40]. Then, the studies of Efraím Hernández-Xolocotzi and Alfredo Barrera settled the bases of the main contemporary intellectual streams of ethnobotanists in one of the countries more prolific of the world in this research field [41–43].

During its early stages, the modern Mexican ethnobotany dedicated most of its efforts in documenting nomenclature and information about use of plants, particularly medicinal plants [37, 39]. At present, ethnobotanical research comprises a broad spectrum of theories and views nurtured with methodological approaches from botanical [44], ecology [45–51], evolutionary ecology [52–57], and anthropological perspectives [8, 58–62] as well as methods developed several decades ago from the ethnobotany itself [45, 63, 64]. All these theories and methods have had an enormous contribution to understanding the complex issue of investigating the interactions and interrelationships between humans and nature, particularly humans and plants, which is a research field recognized as a main stream and basements in the development of social–ecological studies (see a compilation of studies in Berkes and Folke 2000 [65]; and a review for Mexico in Casas et al. 2014 [1]).

The most influencing work on the Mexican ethnobotanical science was undoubtedly the studies conducted by Efraim Hernández-Xolocotzi (1913–1991). His studies started with the traditional agricultural systems, the first studies of Mexican vegetation and the earliest steps of the Mexican ecology [66]. Through these elements, Hernández-Xolocotzi articulated several research approaches that allowed recognizing a particular value to the indigenous knowledge, and with such a consideration, the importance of enhancing ethnobotany in academic research and educational centres. This context favoured a new generation of researchers and studies in ethnobotany and established that Mexico is at present one of the regions of the Americas with a higher number of ethnobotanical studies [44–46, 63, 67–70]. In parallel, advances in ethnobotanical research made possible new paradigms, theories, and methods that currently have configured a particular panorama of the state and perspectives of this research field.

In the context of the global environmental and cultural crisis currently occurring [71–73], since the last quarter of the twentieth century, ethnobotany and ethnobotanists throughout the world aspired to construct an “after description” discipline. The main challenge is that ethnobotany can be able to analyse cultural, social, economic, ecological, and evolutionary patterns in relation to plant use and management in order to more strongly contribute to sustainability science [1, 74]. Hypotheses started to be tested, and rigorous qualitative and quantitative systematic methods become important tools for progressively deeper research approaches. Descriptive studies continue having an important place in ethnobotanical research and should not be sub-estimated. The high theoretical constructions are those with strong descriptive bases [75]. The new ethnobotanical approaches allowed the construction of a stronger theoretical science synthesizing anthropological, archaeological, botanical, ecological, and evolutionary questions and interdisciplinary interactions to answer complex questions [76]. In addition, the new ethnobotany developed in the context of new paradigms in relation to property rights on both knowledge and resources. In the Earth Summit or Río Conference of 1992, organized by the United Nations Conference on Environment and Development (UNCED), new challenges for governments, people, and scholars working in relation to regulations on access to collective knowledge and natural resources in benefit of private interests were established (see [77, 78]). This new stage included in ethnobotanical researches new ethical elements that guided ethnobotanists to conduct their researches and publishing information according to the conditions benefiting the communities rather than private industry. The controversy about this topic continues and conclusions are still difficult to be established, but researchers had to respect new conditions and conveyed with indigenous communities and started to think how their researches may contribute to benefit local people.

Why a Book on Mexican Ethnobotany?

Ethnobotany in Mexico has been particularly active and has influenced theories and methods of this science in different regions of the world. The time of a reflexion of both theoretical and methodological ethnobiological approaches has started, but it requires higher efforts. This book compiles studies of several scholars representing part of researchers of Mexican ethnobotany. It is therefore a general and incomplete panorama of the Mexican ethnobotany; the book aspires to make a modest contribution to that complex task. But in Mexico, ethnobotany has contributed to theoretical, methodological and ethical issues of other anthropological and biological sciences. Particularly important is perhaps its early reflexion about the need of interdisciplinary research [40, 42, 70], the understanding of the complexity of social–ecological interactions, and the importance of linking theoretical and basic science with problems and application of knowledge to solutions of problems [1].

Nowadays, these reflexions are particularly important in the context of the environmental crisis expressed in global change, loss of biodiversity, and human cultures [73]. The highest impact of humans on global ecosystems has happened from the 1950s, more intensely than never in the humans' history on the planet [72, 73]. Industrialization and the hegemonic models of development and patterns of consumption are undoubtedly the main motives of such a crisis. But in this context, ethnobiological sciences have probably more than ever a high responsibility. Documenting local knowledge and techniques are topics extraordinarily valuable in the era of sustainability science [1]. Human experience of interacting with resources, functions, and ecosystems is much longer than the period of the human destruction of the world. Therefore, its contribution in problems solutions may be particularly high. Knowing alternative knowledge, practices, values, and forms to conceive the world are extraordinarily valuable at present [1]. In all these aspects, humans may more probably find the way of alternative forms to face the challenges that make uncertain the future of the World.

The Mexican ethnobotany of the twenty-first Century should focus its attention on understanding social–ecological systems, with emerging properties, the role of local knowledge and trans-disciplinary interactions between the different sectors of the society for constructing agreements for designing a viable future of the planet based on sustainable science [1, 79, 80]. This book aspires to contribute with a panorama of what Mexicans and non-Mexicans have contributed to document knowledge, conception and practices of Mexican cultures around the plant world, and the connection of this science with the sustainability science.

Chapters 2 and 3 provide a general panorama about history and development of ethnobotany in Mexico [81, 82], the main academic institutions conducting ethnobotanical research, the human cultural groups studied, as well as the different approaches and methodological orientations developed in Mexico. Camou et al. provide information about trends of methodological approaches and a reflexion on the perspectives of ethnobotany in Mexico. In the Chap. 3, Bye and Linares analyse the importance of ethno-historical sources, in documenting the development of traditional botanical knowledge and for establishing bases of ethnobotanical theory for understanding of interactions between people and plants in Mesoamerica, but also in other parts of the world.

Chapters 4, 5, and 6 allow deeper and more specific information about the broad spectrum of wild and cultivated edible plant resources of Mexico; in addition, some important particularities of the agricultural systems in which these plants are produced and managed. In chapter 4 [83], Zizumbo et al. show information of the agro-alimentary system of Western Mexico, whose origins are from the archaic period, continued during the pre-Columbian times and the Spanish Conquest. In this chapter, the authors analyse the consequences of changes in human cultural patterns associated to the adoption of other plant resources. A careful compilation of archaeological, ethnographic, and ethnobotanical information allows discussing the relation of diet as motive of domestication of the most important edible plants of Mesoamerica.

In chapter 5 [84], Mapes and Basurto discuss how the diversity of edible plant species is mainly the result of the interaction between biological and human cultural diversities. It illustrates that nearly 25 % of the Mexican flora is used by Mexican people and nearly 30 % of these species are edible plants. This chapter provides information for discussing about changes in current patterns of food, as well as factors explaining the persistence of particular elements characteristic of the rural peoples' diet.

In Chap. 6 [85], Salazar et al. analyse the food system of the lowlands of the Maya of Yucatán, as a result of the integration of the Mesoamerican multi-crop system called "milpa", the South American "conuco", and home gardens. Specifically, this chapter examines the composition of ingredients of the main stoves and regional beverages, finding that their main provenance is from the milpa system and homegardens. The authors question the sustainable viability of the models based on intensive high productivity of the milpa. For the contrary, they emphasize the exceptional value of the traditional milpa not only as a provider of food, but also as a space that creates and re-creates the local human culture.

Traditional markets in Mexico are valuable expressions of the interrelationships between biological and cultural diversities. In the Chap. 7 [86], Linares and Bye provide a panorama of the high richness of plant resources found in these systems, as well as the dynamic building of spaces that are used for coexistence, interchange, and commercial relations from a historical perspective, from the pre-Hispanic tianquiztli (markets in Náhuatl language) to the current "plazas". This study particularly analyses how the demand of wild plants, including endangered species, satisfy diverse needs, in particular social and economic contexts.

Chapters 8–11 allow a general view about Mesoamerican processes of domestication, a crucial expression of interactions between humans and plants. The studies include regional perspectives of plant management; particularly, this is the case of the Tehuacán Valley, one of the richest areas of Mexico in ethnobotanical information and among the oldest and most complete archaeobotanical records. Casas et al., in the Chap. 8 [87], analyse the cultural motives of plant management, as well as the influence of other social, economic, and ecological factors. This chapter illustrates how ethnobotanical studies may make valuable contributions to the theoretical understanding of origins of domestication as well as to practical tasks for sustainable management of forest resources. Throughout history, rural communities have constructed strategies and techniques to manage particular resources and social–ecological systems highly adapted to local conditions and more environmental friendly than industrial processes. Modern techniques are selectively adopted and such adoption may result in hybrid management forms and continual innovation that may be crucial for constructing sustainable future.

Chapter 9 shows a general panorama on the patterns of domestication of plants in Mesoamerica. Pickersgill [88] reviews archaeological and botanical information for different regions of Mexico and different plant species domesticated in the area. Particularly, the cases of species of squashes, beans, maize, chili pepper, amaranth, prickly pears, agaves, and cocoa are analysed, allowing identifying domestication as a relatively slow process at the early stages, but that in relatively short time more and more species were included into the process. When the Europeans arrived to the Americas, the Mesoamerican cultures had developed in the area an impressive spectrum of variation of the species analysed and more than 100 other crop species [89].

In Chap. 10, Blancas et al. [90] show a case study conducted in indigenous communities of the Sierra Negra, a region neighbouring the Tehuacan Valley, analysing motives and factors influencing decision making about plant management. The authors identify ecological, socio-cultural, and technological factors that influence the level of intensity in which plant resources are managed. These factors are mainly related with the scarcity and/or uncertainty in the availability of plant resources and the consequent responses, either individual or collective, in order to ensure their spatial and temporal availability. The authors found that the intensity of plant management is closely related to the role of plants in people's subsistence and their perception about their uncertain availability. Based on their study, the authors conclude that biological and ecological variables such as life cycle, reproductive system, distribution, and abundance, as well as type and number of parts used motivate regulations and forms of management. Management decision involves strategies mainly directed to decrease uncertainty. Similar case studies would allow understanding processes that left to domestication in the past and at present. But in addition, these studies contribute valuable information for sustainable management.

In Chap. 11, Casas et al. [91] show a general panorama of studies on processes of incipient domestication in several regions of Mexico. Several groups of plants are analysed, among them are the "quelites", a term derived from the Náhuatl word "quilitl" involving young edible leaves, flowers, and fruits mainly from herbaceous plants, which are important part of diet among Mesoamerican indigenous groups. Most of them are gathered from wild and weedy populations, but some species are managed and under artificial selection. This chapter also analyses the cases of several species of trees under silvicultural management involving artificial selection in favour of phenotypes desirable for people among individuals composing originally wild forests. Throughout time, this practice may cause incipient domestication, differentiating silvicultural managed and wild populations. This conclusion is particularly relevant since it illustrates that at least in Mesoamerica, but most probably in other main areas of domestication of plants of the world, domestication process could have started before practicing on them intensive cultivation. The authors discuss the hypothesis that Mesoamerica could have been a complex net of microcentres of domestication that deserve to be analysed more deeply.

In Chap. 12, Vibrans [92] analyse the role of weeds in traditional agricultural systems of Mexico. Weeds conform a broad group of plant species that are highly important for rural indigenous people of Mesoamerica and that paradoxically the modern agriculture has underestimated. Weeds in México are intimately linked to cultivation of maize in the traditional multi-crop system “milpa”; numerous species have different degrees of human cultural importance and are managed at different intensities according to their importance degree. As a consequence of such a process, several weedy species exhibit features of divergence from wild or weedy unmanaged plants, showing signs of in situ artificial selection. Most species of managed weedy plants are food resources, but medicines, fodder, and ornamental plants are also included. The study of this chapter contributes information about the role of weeds in the economy of people and as part of decreasing risk strategies.

Chapters 13–18 review researches conducted with different approaches about the role of humans in domestication and diversification of the main Mesoamerican crops. These studies include ecological, genetic, archaeobotanical approaches, all of them emphasizing the role of ethnobotany in the arising of questions and hypotheses to test, interpretation of data and new hypotheses on the processes of domestication, their origin and diffusion.

In Chap. 13, Aguirre and González-Rodríguez [93] analyse through phylogeographic and population genetics approaches questions about origins and diffusion of trees propagated through seeds and vegetative parts. The authors examine phenomena like bottle necks, introgression, geographic origin, and identity of wild relatives of crop species. Ethnobotany and ethnohistory are used as methodological bases for interpreting the result of a complex history revealed by molecular markers.

Chapter 14 covers a multidisciplinary view for studying domestication of plants in the neo-tropics. Specifically, Debouck [94] analyses several species of beans, plant resources of particularly high importance, but not only in their centres of origin in Mesoamerica and the Andean regions. Beans are essential part of the culinary culture of numerous human groups. The chapter analyses the local nomenclature of beans and how combining gloto-chronology and archaeobotanical records is possible to reconstruct some of the regions of origin of the main varieties of edible beans. In addition, in this chapter some hypotheses are explored about the reasons that left to domestication of beans, among them include the nutritious value, the wide range of distribution, tolerance to drought, and its attachment to maize cultivation. In this way, the relation between beans and humans may be seen as an advantageous interaction for both species, which favoured its expansion.

Chapter 15 analyses the case of species of the genus *Cucurbita*, including squashes and pumpkins. In this chapter, Lira et al. [95] analyse and discuss the antiquity of domestication of *Cucurbita* spp., as well as the main motives of artificial selection causing divergence from their wild ancestors. They also analyse the possible regions where the earliest processes of domestication occurred, and the role of these crops in the structuration of the complex agricultural systems “milpa” in Mesoamerica. Finally, the authors discuss the potential risk of native genetic variation in both wild and cultivated contexts caused by the release of genetically modified organisms. Some topics about biosafety that should be taken into account are included in this discussion.

In the Chap. 16, Aguirre-Liguori et al. [96] review molecular studies analysing processes of domestication, phylogeography, and evolution of maize. Maize and its wild relatives, teosinte species, have wide levels of genetic variation and strong signs of local adaptation. One main question is how maize became adapted covering from 0 to 3800 masl. A hypothesis discussed by the authors is that this fact was possible because of adaptive introgression with teosintes from highlands. However, this hypothesis is still inconclusive and ethnobotanical studies might contribute to document useful information, particularly in relation to mechanisms of artificial selection directed to allow adaptive success.

Chapter 17 is dedicated to analyse domestication of chili peppers, particularly varieties derived from *Capsicum annuum*, the most important species of this genus domesticated in Mesoamerica. Pickersgill [97] discusses that the domesticated peppers evolved from the wild pepper called in Mexico “chile piquín”, which, similarly as other wild relatives of crops, are in process of genetic erosion as consequence of the loss of natural habitats and in the case of chiltepín because of its over-exploitation for commercialization. The current fragmentation and disappearing of wild populations make difficult the original areas where *Capsicum annuum* became a crop, and how this process took place. An important aspect to clarify this question is distinguishing and comparing features of wild and domesticated chili peppers. Different research tools have been used to make clear what happened, including archaeobotany, ethnohistorical sources both pre-Columbian and Colonial, together with botanical and particularly genetic information about distribution of variation and phylogeographic approaches. The author concludes that it is inconvenient to direct all efforts in ex situ conservation to stop the genetic erosion. It is rather necessary to take into account human cultures using and managing these plant resources and designing in situ strategies of conservation. Ethnobotanical studies may be particularly relevant to contribute to document human cultural criteria of management and selection and fine details about use and techniques implemented in production systems such as milpas and homegardens in order to design culturally viable planning of in situ conservation of chilli peppers in México.

Chapter 18 is dedicated to analyse the case of another important crop of the world: cotton. In this chapter, Wegier et al. [98] document the traditional uses, those considered in modern industry and those considered as potential uses, from textile fibres to pharmaceutical products. A considerable amount of literature has been produced about the domesticated species and varieties, but relatively few about their wild relatives; hence, the importance of investigating the genetic diversity, interactions with pollinators, pests, and the traditional knowledge associated with cotton’s cultivation. Among the strategies for conserving cotton species and their wild relatives, particularly important are regulations for ensuring biosafety in order to maintain genetic variation in their centres of origin and diversification.

The final chapters of this book provide different perspectives of crucial contemporary ethical aspects in ethnobiological aspects, which also require multi- and interdisciplinary approaches. In chapter 19, Saynes-Vásquez et al. [99] analyse the processes of losing traditional ecological knowledge (TEK) in diverse biocultural regions of Mexico. Among the main causes of this phenomenon, the authors discuss pre-Colonial intercultural conflicts as well as others derived from Colonial and post-Colonial interventions. Particularly, the authors propose new and practical methods to evaluate losing of traditional botanical knowledge in Zapotec communities of the Tehuantepec Isthmus, Oaxaca in southwestern Mexico. In order to analyse more deeply this topic, the authors emphasize the need of linking the cognitive anthropology, the socio-linguistics, and ethnobiology in a historical context.

In chapter 20, Dávila et al. [100] discuss the importance of ex situ conservation for contributing in efforts of protecting the diversity of phyto-genetic resources, based on their ethnobotanical importance. The authors analyse the pertinence of this conservation strategy under the premise that protecting germplasm of plant populations is important to human beings in addition for protecting the information associated to germplasm. The urgent need of conserving and protecting Mexican germplasm is coupled to the velocity of changes and dramatic modification of habitats occurring in this country. Consequently, conservation of biological diversity within species of useful plants favours the protection of cultural diversity.

In chapter 21, Acevedo et al. [101] show the worries among several sectors of the Mexican society before the potential risk caused by the development and use of biotechnological products, particularly in mega-diverse regions considered centres of origin and diversification of important crop species, as it is the case of Mesoamerica. In these types of areas, results are imperative establishing contexts in practices and regulations of biosafety. Until present, local legislation in Mexico has weaknesses and inconsistencies with general, imprecise, and ambiguous norms. Establishing of biosafety measures should be developed considering the analysis of risk, as well as adequate contexts of protection of the genetic capital harboured in México and the Mesoamerican region. This latter task involves enormous challenges for in situ conservation, not only of local varieties of different crops, but also of their wild relatives.

Finally in the Chap. 22, Larson et al. [102] analyse the plant genetic resources as cultural heritage that deserves protection under the principles of human rights. The authors particularly discuss that the cultural heritage has been asymmetrically benefited private companies more than local cultures that have developed varieties throughout a complex biocultural history. The authors analyse and discuss the legal and ethical aspects that should be taken into account to build frameworks of protection and use of plant genetic resources based on the respect of culture and human rights.

Perspectives

We are conscious about the need to include more topics and authors in order to achieve a more complete panorama of the Mexican Ethnobotany. This is, for instance, the case of a deeper analysis about use, management, and economic meaning of medicinal plants. Other important topics are the experiences of the communities in maintaining their plant resources and those about the complexity of traditional systems of classification of plants. It is our intention to continue our current project to include all these topics in a second volume of the Mexican Ethnobotany. However, we consider that the studies published in the following pages of this book contribute to a general and at the same time integrated panorama of the ethnobotanical studies that are enhanced in México, which may be of interest for scholars, students, general public, and those in charge of making decisions in relation to environment and natural resources. The editors of this text are convinced that diffusion and communication of implications of ethnobotanical studies in visualizing alternatives to the hegemonic model of using nature will contribute to constructing a different future more respectful to local cultures and the adequate rhythms of recovering plant populations and biotic communities. We aspire that these premises may become part of public policies for conserving and using plant resources.

With more than one Century as modern scientific discipline and several centuries of empirical research field, ethnobotany is currently a vigorous science throughout the World. As it was reviewed in this text, ethnobotany has been particularly active in Mexico and other areas of Latin America like Brazil, Argentina, Colombia, Peru, and Bolivia [103–111]. Such active research has been favoured by the development of local research institutions (see [81], Chap. 2 of this volume), enhancing academic efforts to generate information and scholar working in the field. It has been relevant to the influence and direct contributions of international research institutions [69]. However, particularly important is the occurrence of high cultural and plant diversities that model highly rich settings of biocultural construction processes [7, 11]. In its beginnings, ethnobotany has been particularly benefited by the development of biological and anthropological approaches and their interactions (predominantly multidisciplinary interactions) for several decades. However, more intensive, real interdisciplinary interactions for understanding particular questions are still possible and desirable among these research fields. Biologists have acquired some anthropological frameworks and methods, whereas anthropologists have looked for ecological and biological frameworks and methods, but the interdisciplinary interaction between biological and anthropological specialists could result in a stronger understanding of phenomena and developing of theory. In addition, the construction of trans-disciplinary research approaches, although frequently claimed, has been scarcely carried out. Ethnobotany as ethno-sciences in general are probably research fields more clearly requiring the interactions of different nature knowledge (traditional, academic, governmental, non-governmental).

Ethnobotany is strongly linked with ethnobiological and ethnoecological research fields; in fact it has been considered part of these areas [111]. In addition, ethnobotany is also strongly related with: (a) Ecological and evolutionary studies, particularly through the studies about the human influence on distribution and abundance of plant species and the configuration of ecosystems. Also, in relation to the evolutionary processes associated to domestication and, importantly, establishing the bases for sustainable management of forest products, functions, and ecosystems.

(b) Archaeology and anthropology also in relation to understanding domestication and origins of agriculture, as well as in relation to symbolism, classification, traditional knowledge, and cosmovision of the plant world for and by people. (c) Ecological economics and sociology, particularly in relation to studies of the governance of forests and forest resources as common goods. Within each of these research fields, there are constellations of questions that require disciplinary interactions; therefore, ethnobotany is eminently an interdisciplinary research field that requires to be developed in such a way.

An important approach moving on ahead the development of ethnobotany is science for sustainability. This approach recognizes the need of constructing alternative forms of developing science including issues such as sustainability and resilience of socio-ecological systems, trans-scales or occurrence of phenomena at different dimensions influencing emergent properties of the systems, and complexity of both ecological and social phenomena in interaction. All of these issues require emergent scientific approaches such as inter-disciplinary (interactions among disciplines for understanding a problem in common), trans-disciplinary (which recognizes the value of knowledge systems constructed by different sectors of society, not only scientific institutions, and the need to synthesize both knowledge and praxis experiences for projecting new agendas of participatory research and actions), and adaptive management (which recognizes the high uncertainty of socio-ecological systems and sustainability issues, and proposes more flexible decision making based on knowledge available, systems interventions, and evaluation of the actions performed).

In all these issues, ethnobotany may play important role. For instance, understanding socio-ecological systems is part of the aims of ethnobotany and therefore it may contribute to a general understanding of them, establishing bridges of complex systems through interdisciplinary approaches. Finally, ethnobotany and ethnobiological sciences may be particularly important for establishing connections between the new challenges for attending the global crisis of the World and the human experience accumulated for thousands of years and that are maintained in the traditional ecological and botanical knowledge.

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Chapter 2
Ethnobotany in Mexico: History, Development, and Perspectives

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Abstract Ethnobotany is defined as the study of the traditional botanical knowledge of different cultures, the techniques utilized in the use and management of plant resources, and the place they have in their cultural Cosmo vision. This study aimed to review the development and perspectives of ethnobotany in Mexico, based on an extensive review of all ethnobotanical studies showed at the Mexican Botanical Congress (MBC), the main forum of ethnobotanical studies in Mexico, between 1963 and 2010. We systematized a total of 897 works, identifying their progressive increase in the generation of investigative papers up until 1990, then a decrease until 1995 and a new increase from 1995 to the present. The main Mexican institutions studying ethnobotany are the *Universidad Nacional Autónoma de México*, *Universidad Autonóma Chapingo*, *Instituto Politécnico Nacional*, *Universidad Autónoma Metropolitana,* and the *Universidad Autónoma de Nuevo León*, which produced nearly half of all the studies recorded. The best represented cultural groups studied were the Maya, Nahua, Otomí, Totonac, and Mixtec, studied under the pre-

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dominant approach of descriptive ethnobotany. Ethnobotany in Mexico is in a stage of growth and therefore in the phase of consolidating its approaches, particularly in the areas of ecological, economic, quantitative, and evolutionary ethnobotany. In order to achieve the development of sustainable management strategies of plant resources, it is of the highest priority to consolidate ethnobotanical research and direct it towards the analysis of environmental degradation and solutions.

Keywords Ecological ethnobotany • Economic ethnobotany • Evolutionary ethnobotany • Ethnobotanical approaches • Ethnobotanical history • Quantitative ethnobotany

Introduction

As a scientific discipline, ethnobotany emerged as a result of the co-evolution of botany and anthropology throughout the eighteenth and nineteenth centuries. It was, however, in the twentieth century when it became a consolidated study field with unique methods. Harshberger [1] first coined the term ethnobotany and defined its domain as "… the study of the interrelationships of primitive man with plants." In the 1930s, interest in economically important species introduced the term "economic botany," which made explicit the interest in linking ethnobotanical research and the prospective of new materials for industry. Oakes [2], for instance, defined economic botany as "… the link between anthropology and industry derived from plants." In contrast, for anthropologists of that time, plants and animals were elements with important cultural significance, and through the study of such significance, anthropologists constructed the early ethnobiological approaches. The anthropologist Maldonado-Köerdell [3] defined ethnobiology as "… responsible for the study of plants and animals, in any region, defined by a human group that inhabits or habituates a region to get them … essentially a cultural science." In the 1940s, ethnobiological research gained status as a discipline focused on the knowledge of plants and animals between different people. Particularly, Schultes [4] defined ethnobotany as an intermediary between botany and anthropology, whose purpose is "…the study of the relationship between humans and their plant environment…". Similarly, Jones [5] defined ethnobotany as the field of study specifically aimed at analyzing the relationship between humans and plants.

These basic concepts have prevailed in subsequent decades, but several authors have incorporated different emphases to definitions according to their perspectives. For example, Bye [6] defines ethnobotany as "… the study of the biological basis of the interactions and plant-human relationships at different levels of organization (ecosystems, communities, individuals) in a geographical, social and evolutionary scale."

Because of the momentum of the ethnobotanical movement, particularly since the 1960s and early 1970s, different research approaches in the field have been developing in Mexico to the present day. This process was reinforced by the recognition of ethnobotany as a scientific discipline, which has been strengthened with robust methodological frameworks and depuration of the field [7–11]. By the 1970s, Latin American ethnobotany succeeded in developing a critique of the folklorist and utilitarian approaches developed mainly by some researchers from the U.S. and Europe. As part of this critique, Hernández-Xolocotzi [7] recognized the interdisciplinary nature of ethnobotany and the importance of "…the collaboration of institutes, professionals interested and trained in accordance with the inherent problems of collection, propagation and conservation." At the end of that decade, Barrera [12] defined ethnobotany as "…an interdisciplinary field that includes the study and interpretation of knowledge, cultural significance, management and traditional uses of the elements of flora"; a concept in which Hernández-Xolocotzi [13] included the dimensions of time and space "… over time and in different environments."

Currently, ethnobotany is a scientific discipline that documents, analyzes, and looks for understanding the botanical knowledge possessed by different cultural groups that inhabit the planet, the beliefs and cosmo vision in relation to the plant world around them, and interactions and practices established with plants to take advantage of their benefits. Such knowledge, beliefs, interactions, and practices are those concepts that Toledo [14] and Berkes [15] have called and defined as "corpus," "kosmos," and "praxis," respectively. These cultural elements have been the result of the development of specific human cultures in time and space and have been passed from generation to generation in oral or written form.

The main interest of this chapter is to provide a perspective about the state of ethnobotanical research in Mexico. For this task, we analyze the main approaches of ethnobotany that drive the development of this field of study in Mexico, and the perspectives, priorities, and strategies necessary to strengthen this area of research in relationship with various sectors of society.

Ethnobotanical Research, a General Overview

Numerous studies have documented traditional ethnobotanical knowledge in Mexico. These include not only utilitarian aspects of the properties of plants, but also aspects such as (a) forms and functions of their component structures, (b) life cycle, (c) behavior in relation to environmental changes (e.g., seasonality in the production of leaves, flowers, fruits, and seeds) [16–18], (d) the vulnerability or resilience to interactions with herbivores and/or competitors or to human activities (burning, logging, and other forms of disturbance) [18–22]. Traditional botanical knowledge (TBK) also includes ecological aspects like distribution and abundance of plants in specific environments, the interactions with other living beings (herbivores, frugivores, bird species that nest in them, species of insects whose larvae feed on their tissues, among others). Such knowledge can be comprehensive and is often used as criteria for classification of plant species or variants in scientific studies; see examples in [23–26], as well as for the development of management strategies [19, 21, 22, 27–30].

TBK of plants has practical application in management techniques that shape human interaction with plant populations and communities and can be classified in different types. The first type is the extraction or harvesting of useful parts of the plants. Of the estimated 5000–7000 of plant species that are currently used by traditional people in Mexico [18], about 90 % are obtained by this kind of interaction [24]. Some ethnobotanical studies have characterized various forms of collection, including those involving community agreements to rotate and protect areas, as well as occasional vs. intensive practices [21, 22, 31, 32]. Furthermore, several studies [19, 33, 34] suggest that extractive techniques may control such factors as size, structure, and population dynamics to ensure and increase the availability of certain plant resources.

A second type of interactions between humans and plants is formed by different silvicultural forms of management. We have generally identified: (a) tolerance, which involves leaving individuals of favorable species when vegetation is purposefully disturbed, (b) promotion or encouragement of favorable species, which involves activities aimed at increasing the population density of favorable species, (c) protection, including control of herbivores, thinning of competing plants, performing pruning and other forms of protection of plants representing some utilitarian advantage for humans in natural vegetation areas subjected to deliberate disturbance, and (d) sowing and transplantation of propagules (sexual or vegetative) or complete individuals from wild environments to humans-controlled environments (such as agricultural plots, orchards, or home gardens) [19, 35–38]. In Mexico, about 700 species of plants have been documented that are subject to some of these types of silvicultural management [28]. However, this figure is likely an underestimate; for example, only in Tehuacán-Cuicatlán Valley, Blancas et al. [39] reported about 600 species under these forms of management.

Silvicultural management has been distinguished from agricultural management [19, 27]. Agriculture constitutes the third general type of interaction between humans and plants. At this level, there are great diversity of species and varieties of plants under traditional management, with a high diversity of agricultural hydraulic and intensive systems (including irrigation systems, raised or drained fields systems, and terraces systems), seasonal and semi-intensive and extensive systems (including high diversity of rain-fed systems and slash-and-burn, shifting or swidden agriculture), as well as homegardens, and agroforests combining wild and domesticated plants (e.g., cocoa, coffee, and pineapple plantations and a wide variety of types of milpa in association with elements of forests) [18, 40–42]. Traditional agriculture may involve management of varieties resulting from modern breeding processes used in intensive agricultural systems.

Mexico is one of the countries on the world with the highest biological and cultural diversities [43–45]. However, one of Mexicans' major concerns is the gradual loss of these diversities, including the threatening processes occurring on species at the community and ecosystems levels, as well as intra-specific variability at population level. These processes of loss are the result of multiple factors influencing the transformation of natural ecosystems and complex processes of causing cultural change [46], which induce the transformation of traditional management systems [42, 47, 48]. Against this backdrop, several authors have considered that for the world today, conservation and construction of sustainable management strategies of natural resources and ecosystems are of high priority. It is also widely recognized that traditional knowledge is particularly important to these goals in the understanding, respect, use, and even improvement of local knowledge and practices to protect global patrimony [15, 47, 49]. This posture recognizes that the traditional forms of natural resource use possess traits of sustainability that must be understood and managed. It also recognizes complexity of the socio-ecological systems in which they are embedded as well as the complex processes of resource utilization that require the inclusion of human experience in the broadest sense, as well as the ongoing evaluation of successes and failures and consequent adjustments. This is the notion of adaptive management, which recognizes that the complexity of socio-ecological systems requires continuous construction, monitoring, and adjustment (adaptation) of intervention strategies of natural resources and ecosystems.

Ethnobiological studies are a window to the understanding of traditional knowledge and practices of management of biotic resources and are, therefore, crucial for technological innovation for the sustainable use of resources and environmental problems resolution. In recent decades, these goals have become increasingly explicit in ethnobiological research, particularly those research approaches that include ecological methods [26, 50–52].

Approaches to Ethnobotanical Research

Miguel Ángel Martínez-Alfaro [53], an outstanding Mexican ethnobotanist, characterized eight general lines of ethnobotanical research: (1) archaeobotany, (2) medicinal plants, (3) edible plants, (4) cognitive studies, (5) forest management, (6) agroforestry systems and orchards, (7) domestication and the origin of agriculture, and (8) historical studies. These perspectives reflect the research fields of ethnobotany, but also they are constructed from particular theoretical frameworks. In this sense, Martínez-Alfaro [53] recognizes that the research approaches referred to above are developed under various disciplines such as taxonomy, plant ecology, plant geography, plant physiology, floristic, among others. Based on the thinking of Martínez-Alfaro [53], in this study we recognize six major areas of theoretical construction of ethnobotany:

1. Descriptive ethnobotany. This approach primarily focuses on constructing listings and catalogs of plants along with their uses and traditional nomenclature.
2. Cultural ethnobotany. This perspective includes studies that analyze historical aspects of the use of plants, their cultural significance, traditional classification systems (folk classifications), linguistic analysis, processes of acculturation, and intra-cultural variation of plant use and knowledge. We also consider within this approach those studies pertaining to knowledge and traditional perception of plant resources and ecosystems, as well as studies that look for understanding the cultural significance and implications of classifications of plants and ecosystems where they occur.

3. Economic ethnobotany. This approach focuses on the economic valuation and marketing of plants (market research and exchange), the commercial and industrial potential of crops and wild plants (phytochemical analyzes, bioprospecting), processes (experimental propagation techniques of crops, among others), analyses of performance, cost–benefit balance, and studies evaluating the role of plants in peasant subsistence.
4. Ecological ethnobotany. This research perspective focuses predominantly on studies that analyze the spatial distribution, abundance, seasonal availability of plant resources, phenological studies, demographic and synecological research, as well as impact assessment for management techniques of populations of useful plants, their communities, and ecosystems. We also included studies aimed at characterizing and evaluating functional aspects of traditional management systems. In this approach, the ecological bases of the use of plant resources and the implications for conservation and sustainable management from the perspective of the ecology of populations, communities, ecosystems, and/or landscape are emphasized.
5. Evolutionary ethnobotany. This approach focuses on studies that analyze the evolutionary implications of plant management. We included researches documenting morphological variability and population genetics, physiological and reproductive variations in wild and managed plants with the goal of understanding the current processes of domestication. Archaeological, systematic, and phylogeographic studies were also included that provide understanding with regard to the evolutionary history of these processes associated with human–plant management, its origin and diffusion.
6. Theoretical ethnobotany. We included those researches that make reflection and construct theories on the ethnobotanical research as a scientific discipline. These studies generally review the development of ethnobotanical research and aspire to define and steer the course of ethnobotany. Our analysis in this chapter exemplifies this research approach.

Approaches to the State of Ethnobotanical Research in Mexico

One of the interests of the present study is to provide a perspective on the state of ethnobotanical research in Mexico. This preliminary outlook is based on the review of the abstracts of the ethnobotanical studies showed in the meetings of the Mexican Congress of Botany (MCB) from 1960 to 2010 (Table 2.1). The works presented at these congresses (including lectures, oral presentations, posters, symposia, workshops, and conferences) were considered as a primary and the most representative source of information on the ethnobotanical studies carried out in Mexico during the period referred to. It is important to clarify that the MCB is divided into thematic areas within which ethnobotany and economic botany were the primary scopes of systematization of the analyzed works. With the information obtained, we constructed a database that included: (1) the institutions at which the authors of the work presented were affiliated, (2) the locations in Mexico where the ethnobotanical

Table 2.1 Meetings of the Mexican Congress of Botany (MCB) between 1960 and 2010

MCB	Year	Date	Place
I[a]	1960	24–26 October	Ciudad de México
II	1963	17–21 September	San Luís Potosí
III	1966	24–28 October	Ciudad de México
IV	1969	8–11 September	Coahuila
V	1972	3–9 December	Ciudad de México
VI	1975	21–26 September	Veracruz
VII	1978	15–21 October	Ciudad de México
VIII	1981	17–23 October	Michoacán
IX[a]	1984	–	Ciudad de México
X	1987	27 October–03 November	Jalisco
XI	1990	30 September–5 October	Morelos
XII[a]	1992	–	Mérida
XIII	1995	5–11 November	Morelos
XIV	1998	18–24 October	Ciudad de México
XV	2001	14–19 October	Querétaro
XVI	2004	17–22 October	Oaxaca
XVII	2007	14–18 October	Zacatecas
XVIII	2010	21–27 November	Jalisco

[a] MCB meetings for which there is no information of the works presented

research was accomplished, (3) the cultural groups studied, and (4) the theoretical framework of the ethnobotanical work analyzed.

We recorded a total of 897 ethnobotanical works presented in 18 sessions of MCB between 1960 and 2010. Figure 2.1 shows a trend of progressive increase in the production of ethnobotanical works, which reach a peak in 1990 and then a drastic decrease. Such marked decline in the production of ethnobotanical works presented at the MCB was influenced by the Ejército Zapatista de Liberación Nacional uprising, which represented the starting point for the visibility and momentum of contemporary peasant and indigenous movements [54] to which ethnobotanists were particularly receptive in the academic sector. From 1995 to 2001, there was an increasing trend in the number of ethnobotanical papers presented at the MCB. Then the number of works descends again and appears to gradually recover by 2010.

A total of 116 institutions participated with ethnobotanical studies over the history of MCB, among them 70 are Mexican (66 %) and 19 are foreign (18 %) educational and research institutions, 11 government agencies (10 %), and 6 NGOs and social organizations (6 %). The ethnobotanical works reviewed in this chapter constitute a sample of the studies carried out in Mexico and mostly done by Mexican researchers and research institutions. However, Martínez-Alfaro [53] estimated that about 50 % of ethnobotanical studies in Mexico are carried out by foreigners, so this bias must be considered in the data presented here. This information indicates that

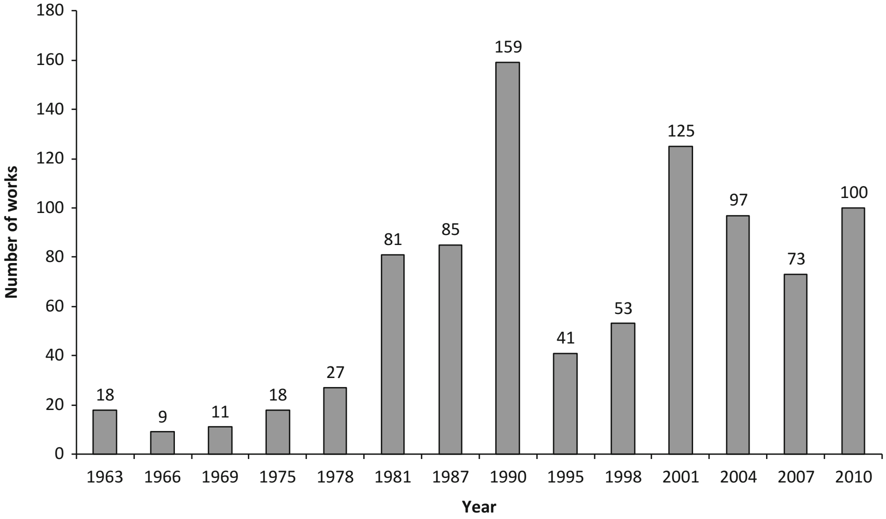

Fig. 2.1 Number of ethnobotanical works presented at the meetings of the MCB between 1963 and 2010

non-Mexican researchers and institutions developing ethnobotanical research do not regularly attend the MCB.

Among the most relevant institutions contributing with ethnobotanical works, we found the *Universidad Nacional Autónoma de México* (UNAM) with 244 studies over the period analyzed (26 %), the *Universidad Autónoma Chapingo* (UACh) with 81 (9 %), the *Instituto Politécnico Nacional* (IPN) with 63 (7 %), the *Unversidad Autónoma Metropolitana* (UAM) with 52 (6 %), and the *Universidad Autónoma de Nuevo León* (UANL) with 30 (3 %) (Fig. 2.2). About 50 % of the works presented at the MCB were produced by these five institutions located in different cities of Mexico. Other universities with significant contributions are: *Universidad Autónoma de Yucatán,* UADY (22 works), *Universidad Autónoma del Estado de Morelos*, UAEM (21 works), *Universidad de Guadalajara*, U de G (20 works), *Universidad Veracruzana*, UV (19 works), *Benemérita Universidad Autónoma de Puebla*, BUAP (17 works), *Centro de Investigación Científica de Yucatán,* CICY (15 works), and the *Universidad Autónoma del Estado de Hidalgo*, UAEH (14 works).

It appears that not all the Mexican institutions carrying out elatterthnobotanical studies are well-represented in the MCB. These are, for instance, the cases of the *Instituto Tecnológico del Valle de Oaxaca*, ITVO (with 4 works) and the *Colegio de la Frontera Sur*, ECOSUR (with 3 works), which have recognized research groups in the area of ethnobotany and ethnobiology, and are poorly represented in the MCB.

Of the 31 states that make up the Mexican nation, there has been at least one ethnobotanical study in 30 of them. The states with the highest number of studies are: Puebla (102 works), Oaxaca (70 works), Veracruz (53 works), Yucatán (43 works), Morelos (34 works), Guerrero (31 works), Tabasco (28 works), State of Mexico (26 works), and Hidalgo (26 works) (Fig. 2.3). The states that showed the lowest number of studies were: Guanajuato (2 works), Sinaloa (2 works), and

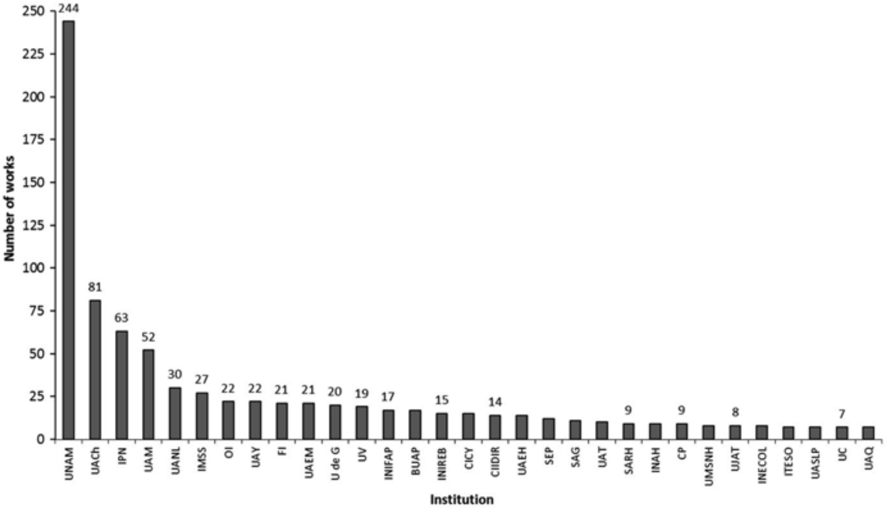

Fig. 2.2 Papers presented at the MCB (1963–2010) per institution. Universidad Nacional Autónoma de México (UNAM), Universidad Autónoma de Chapingo (UACh), Instituto Politécnico Nacional (IPN), Universidad Autónoma Metropolitana (UAM), Universidad Autónoma de Nuevo León (UANL), Instituto Mexicano del Seguro Social (IMSS), Other Institutions (OI), Universidad Autónoma de Yucatán (UAY), Foreign Institutions (FI), Universidad Autónoma del estado de Morelos (UAEM), Universidad de Guadalajara (U de G), Universidad de Veracruz (UV), Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), Benemérita Universidad Autónoma de Puebla (BUAP), (INIREB), Centro de Investigación Científica de Yucatán A.C. (CICY), Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional—IPN (CIIDIR), Universidad Autónoma del Estado de Hidalgo (UAEH), Secretaría de Educación Pública (SEP), Secretaría de Agricultura y Ganadería (SAG), Universidad Autónoma de Tamaulipas (UAT), Secretaría de Agricultura y Recursos Hidráulicos (SARH), Instituto Nacional de Antropología e Historia (INAH), Colegio de Postgraduados (CP), Universidad Michoacana de San Nicolás de Hidalgo (UMSNH), Universidad Juárez Autónoma de Tabasco (UJAT), Instituto de Ecología A.C. (INECOL), Instituto Tecnológico de Estudios Superiores de Oriente (ITESO), Universidad Autónoma de San Luis Potosí (UASLP), Universidad de Colima (UC), Universidad Autónoma de Querétaro (UAQ)

Nayarit (without any studies recorded in the MCB). This fact is important to highlight because the ethnobotanical research group of the *Facultad de Ciencias* (UNAM) has developed research projects particularly in this latter state, which is not reported in the works reviewed.

The revised works include a total of 42 indigenous cultures, including studies on the Quechua in Peru and the Kekchi in Guatemala. Indigenous cultures best represented were the Maya (39 works) (Fig. 2.4) followed by the Nahua (33 works), Mixtec (21 works), Otomí (20 works), Totonac (18 works), and the Zapotec (12 works). Indigenous cultures underrepresented (only one registered study each) are the Chol, Huichol, Ixcatec, Matlatzinca Mayo, Pima, Seri, Tlapanec, Tlaxcaltec, Tzeltal, and Yaqui. Nearly 74 % of the abstracts made no reference to any indigenous cultures in particular, which is apparently because the studies were conducted with Mestizo people.

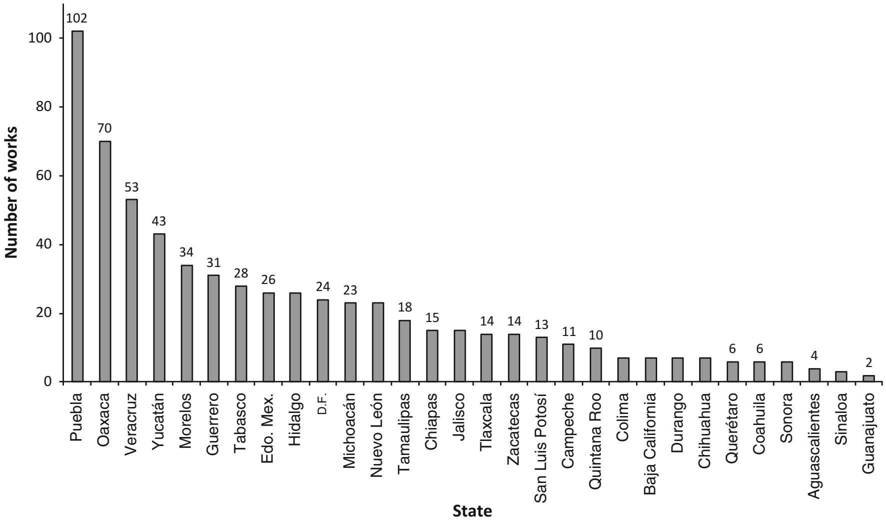

Fig. 2.3 Ethnobotanical works presented in the MCB (1963–2010) by state

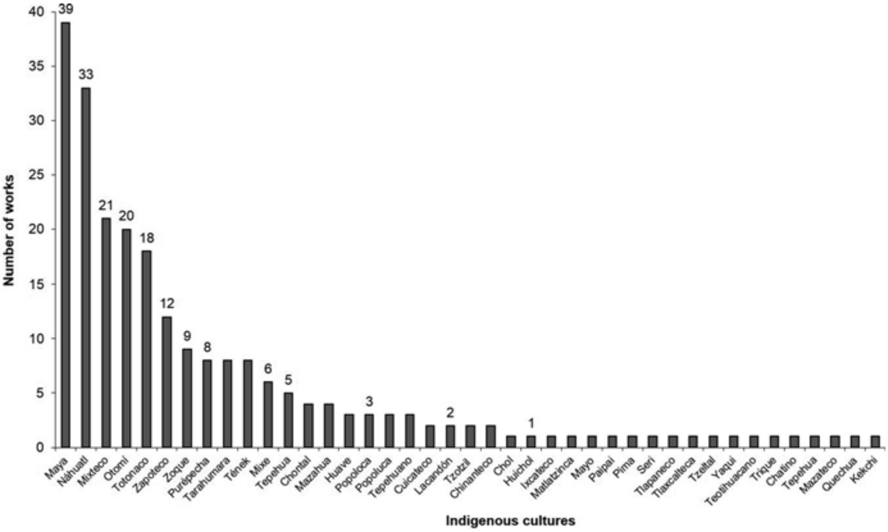

Fig. 2.4 Papers presented at meetings of the MCB (1963–2010) by indigenous cultures

Table 2.2 shows the total number of studies recorded in the Ethnoecological Atlas database [46, 55] relative to those recorded in the MCB and takes into account the most represented original cultures. Although the Ethnoecological Atlas includes information from different fields of knowledge (not just from the ethnobotanical perspective), the Maya, Nahua, Mixtec, Totonac, and Otomí are also the best represented, which is consistent with findings in our MCB sample. To date, there have been studies on 40 of the 68 indigenous groups [56], and 56 % of the total have

Table 2.2 Works reported in the Ethnoecological Atlas vs. the ethnobotanical works presented in the MCB between 1963 and 2010

Cultural group	Ethnoecological atlas[a]	MCB
1. Maya	596	39
2. Nahua	238	33
3. Purépecha (P´urhépecha)	151	8
4. Zapoteco (Ben´zaa o binnizá o bene xon)	129	12
5. Chontal (Oaxaca y Tabasco)	102	4
6. Tzotzil (Batzil K´op)	100	2
7. Mixteco (Ñuu Savi)	96	21
8. Totonaca (Tachihuiin)	85	18
9. Otomí (Ñahñú o hñä hñü)	71	20
10. Tarahumara (Rarámuri)	71	8

[a]Toledo et al. (2001)

focused on only five of them. From the perspective of the two sources of information, the need for more ethnobotanical studies including a greater number of the Mexican original groups is clear.

In the 1960s, the studies focused on economic ethnobotany and ecological ethnobotany approaches dominated the ethnobotanical research in Mexico. Only these two approaches covered 28.6 % (6 works) and 47.6 % (10 works), respectively, of the papers presented in the 1963 MCB (Table 2.3). In that decade, the studies covering descriptive ethnobotanical approaches, cultural ethnobotany, evolutionary ethnobotany, and theoretical ethnobotany were scarce (Table 2.3). However, from the 1970s, there has been a gradual increase in the number of ethnobotanical work using the different approaches considered in this analysis. The proportion of research with a descriptive approach went up in the late 1970s becoming the predominant approach at the MCB (29 papers on average per conference) followed by economic ethnobotany (18 papers), cultural ethnobotany (17 papers), ecological ethnobotany (16 papers), evolutionary ethnobotany (3 papers), and theoretical ethnobotany (3 papers on average per conference) (Table 2.3). It is noteworthy that, since 1990, there has been a trend toward presenting a more even proportion of the papers pertinent to the different ethnobotany research approaches at MCB conferences.

The scope of the analysis presented here represents only a sample of the ethnobotanical production in Mexico mainly by Mexicans and not all the research generated either by national or foreign educational and research institutions. Moreover, understanding the interests and motivations of the ethnobotanical research in Mexico is incomplete from the characterization of the theoretical approaches that we have made. We recognize that a limitation of our analysis is the review of only the abstracts of works presented at the MCB (which is the information available in the reports of the congresses that were reviewed) and also that we identified that other research areas developing etnobotanical studies (for instance, anthropologists) are not well-represented in the MCB. Therefore, to have a more complete picture of the development of ethnobotany in Mexico is necessary to expand the sources of analysis (including theses, scientific articles, books, interviews, among others). However, the trends and proportions identified based on this source allow

Table 2.3 Number of papers presented at the MCB between 1963 and 2010 by each ethnobotanical research approach

Year	Descriptive	Cultural	Economic	Ecological	Evolutionary	Theoretical
1963	3 (14.3)	1 (4.8)	6 (28.6)	10 (47.6)	0	1 (4.8)
1966	2 (22.2)	0	6 (66.7)	1 (11.1)	0	0
1969	2 (18.2)	0	2 (18.2)	5 (45.5)	2 (18.2)	0
1975	6 (28.6)	0	6 (28.6)	4 (19.0)	2 (9.5)	3 (14.3)
1978	14 (40.0)	4 (11.4)	8 (22.9)	5 (14.3)	1 (2.9)	3 (8.6)
1981	30 (27.0)	21 (18.9)	20 (18.0)	35 (31.5)	1 (0.9)	4 (3.6)
1987	48 (39.7)	24 (19.8)	32 (26.4)	16 (13.2)	0	1 (0.8)
1990	78 (35.8)	46 (21.1)	41 (18.8)	33 (15.1)	12 (5.5)	8 (3.7)
1995	16 (32.0)	11 (22.0)	11 (22.0)	7 (14.0)	2 (4.0)	3 (6.0)
1998	24 (32.9)	12 (16.4)	16 (21.9)	18 (24.7)	3 (4.1)	0
2001	35 (35.0)	23 (23.0)	18 (18.0)	17 (17.0)	5 (5.0)	2 (2.0)
2004	38 (31.9)	24 (20.2)	33 (27.7)	17 (14.3)	6 (5.0)	1 (0.8)
2007	50 (39.4)	27 (21.3)	17 (13.4)	30 (23.6)	3 (2.4)	0
2010	55 (34.8)	44 (27.8)	31 (19.6)	22 (13.9)	4 (2.5)	2 (1.3)
Annual average	29	17	18	16	3	2

The number in parentheses represents the ratio of works per year

identifying the heterogeneity of the development of the research approaches and those cultural groups and ecological regions that need to be studied.

Ethnobotanical Research Perspectives in Mexico

Ethnobotany currently faces challenges that lie beyond the scientific activity and encourages reflection on the academic work of ethnobotanists. In the twenty-first century, ethnobotany has a wide range of applications and roles in society that easily exceed the scientist work. It has a strategic position in the search for solutions to environmental problems and faces philosophical, ethical, epistemological challenges in local and global challenging contexts [53, 57]. As in the context of other disciplines, and particularly ethnosciences [58, 59], there are three useful paradigms that can guide the ethnobotanical research.

Sustainability Science

At a first level, seeking sustainable management of natural resources elucidates the need to develop models that: (1) maintain and restore the natural resources and ecosystem processes, (2) strengthen the social organization of the sectors that interact with ecosystems and resources, and (3) generate more equitable economic processes [60–62]. In the scientific literature, there are numerous references to the great difficulties in operationalizing the concept of sustainability. Among other limiting factors, the specialization and reductionist methods that dominate contemporary scientific research can be mentioned [63, 64]. Due to the complexity of common epistemic frameworks articulated under different fields of knowledge, another of the great challenges is to include the participation of different stakeholders in addressing socio-ecological problems, as well as the attention to the various scales at which they occur [63–66].

Several authors have raised the need to develop a sustainability science [67] whose essential features are recognized to be: (a) that the problems associated with natural resource management must be viewed from a systemic point of view, both from a social and ecological perspective, as these form all socio-ecological systems, (b) the design of interventions in these systems requires interdisciplinary interaction and the participation of different social sectors, (c) such approaches must consider operating processes in trans-scalar systems, and (d) the complexity of the systems and the high level of uncertainty that exists requires the adoption of interim intervention schemes subject to ongoing assessments of experiences and effects (adaptive management).

In the context of sustainability science, ethnobotany has much to contribute. The information documented through the research approaches considered in this study are of great relevance in making decisions about harvesting resources and techniques as well as the socio-economic and ecological implications of such use. Ethnobotany also has a close relationship with community development processes among its many purposes; an important one is analyzing the different dimensions of production in terms of natural, economic, and socio-cultural implications and significance [68, 69].

Participatory Research and the Dialogue of the Different Forms of Knowledge

Ethnobotany encourages the process of community participation in the management and administration of natural resources. One of the major obstacles in solving environmental problems is the lack of participation [70, 71]. Through participatory processes, it is feasible to generate horizontal and reciprocal relationships within the community and external agents to strengthen the social fabric and decision-making related to the use and enjoyment of natural resources [72]. Today, there are many participatory approaches seeking sustainability with regard to the exploitation of natural resources [73, 74] and they are useful for visualizing the cross-interaction networks that must be woven together to successfully achieve the project objectives.

Conventionally, transfering of information and technology arising from research institutions has been unidirectional and flowed top-down [75]. This process has led to confrontations in at least two different knowledge structures putting peasant knowledge in opposition to technical–scientific Western perceptions [76]. This has often resulted in significant cultural transformation [77–79].

While ethnobotany may significantly contribute to sustainable management processes of resources and ecosystems, as well as reassessing and documenting local management practices, encouraging ownership of "technology" in a particular cultural context implies that it must be related to topics of interest to the community [72]. This approach represents reverse knowledge transfer from a community to other areas (e.g., Academic sectors), with respect for local ideas, arguments, and innovative capabilities as a means to strengthen the processes of organization and community development [80]. In this sense, the dialogue of knowledge paradigm [81, 82] is an approach that is useful for interchange between different social sectors such as no governmental organizations, rural, periurban and urban stakeholders, governmental institutions, and academic sectors. Ethnobotany can and should adopt such paradigm and promote research around wisdom, knowledge, and values in the relationship between plants and human beings with cultural, economic, ecological, political, and social differences.

Cultural transformation affects not only the technological aspects of the appropriation of nature, it also generates changes in social structure, habits, and consumption patterns of land use and resources, which can generate gradual differences between the needs of young and old, between migrants and residents, among original groups and mestizos, etc. [83]. Accordingly, ethnobotany can play an important role in building communication bridges between sectors of a community helping to maintain balanced information exchange and preserve cultural values in rural communities.

Intellectual Property Rights, Bioprospecting, and Biopiracy

Today, intellectual property rights relating to natural resources is a topic of much debate worldwide. It is sparked by conflicts between rural communities generating knowledge, skills, and proprietary of genetic resources on the one hand, and large companies that make use of such resources and knowledge for private profits on the other [84]. The topic is certainly of great importance in the context of respect for cultures, equity, and human rights.

The exploration of biodiversity in search of genetic and biochemical resources with commercial value (bioprospecting) based on traditional knowledge brings with it the issue of biopiracy. Pat Mooney defined the term in 1993 [85] and described it as "…the use of intellectual property to legitimize the exclusive right and control of knowledge and biological resources without recognition, reward or protection of the contributions of indigenous peoples." Biologists and ecologists in general have been signaled from members of academic and non-academic sectors, as voluntary or involuntary partners in the process of bioprospecting, and worse as collaborators in biopiracy. Therefore, there is a social and political demand that ethnobiologists should participate actively in creating alternatives to protect and preserve the rights of the indigenous people on their traditional knowledge and their genetic resources.

According to Toledo [55], in Mexico, there are numerous examples of natural resource management within what he calls "the silent revolution." This movement included nearly 15 years ago more than 2000 cases of ejidos and communities, associations, and cooperatives in over 12 states of Mexico. It is possible to state that this number has significantly increased during the last years because of the social resistance movements including demands in relation to natural resources, property rights of genetic resources, and biosafety. This movement engaged processes like: (1) agroecological and organic products, (2) sustainable forest management, (3) non-timber forest resource extraction, (4) defense of territory and natural resources, and (5) ecotourism projects. Anta and Pérez-Delgado [86, 87] and Toledo et al. [88] documented more than 800 community events in the sustainable management of natural resources in the states of Michoacán, Oaxaca, and Quintana Roo alone. It is precisely in the context of these civil society movements aimed at sustainable management of natural resources, in which ethnobotany's relevance is most pertinent and currently most needed. Its active role in the generation of information to answer questions about the *kosmos*, *corpus,* and *praxis* related to the plant world is of great value to support the processes of technological innovation, social organizational and institutional linkages that can guide local strategies, and policies with the goal of achieving locally and globally sustainability and equity. As well as helping to identify those whose knowledge should be recognized and the knwoledge that should be recognized.

Conclusions

According to the information analyzed, ethnobotany in Mexico experienced a diversification of approaches, a decreasing trend in the 1990s with a recovering during the last decade (2010). The number of studies recorded increased and decreased in different areas, suggesting that Mexican ethnobotany is still dynamically evolving. The information suggests that Mexican ethnobotany emerged closely related to ecological, economic botany, and floristic studies. The predominant approach has been descriptive ethnobotany, focused on a limited number of research institutions, regions, and people. One of the challenges facing this field of research in Mexico is therefore to direct their growth seeking to strengthen the diversity of approaches and research groups, particularly more analytical-focused approaches as well as strengthening research groups especially in institutions that are outside of Mexico City.

Ethnobotany is an area of research that addresses questions regarding *kosmos*, *corpus*, and *praxis* in relation to plants. It combines anthropological, botanical, ecological, and evolutionary approaches, among others. However, it is infrequent that specialists of different disciplines converge, being more common for specialists to penetrate into domains beyond their specialty areas to address their ethnobotanical questions. This condition suggests that ethnobotany is still facing the challenge of developing interdisciplinary interaction mechanisms and further transdisciplinary research approach. The latter are particularly relevant in a research field in which knowledge of cultural groups is the main focus. The development of disciplinary, interdisciplinary, and transdisciplinary approaches is very important to address the issue of strategies for the sustainable use of natural resources and ecosystems.

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Chapter 3
Ethnobotany and Ethnohistorical Sources of Mesoamerica

Robert Bye and Edelmira Linares

Abstract Almost five centuries of interactions and relationships between humans and plants in Mesoamerica have been documented, principally from the etic perspective. This essay focuses on ethnohistorical sources mostly from New Spain (which includes much of contemporary Mexico) during the sixteenth, seventeenth, eighteenth, and early nineteenth century during Mexico's Viceroyalty period. Indigenous documents usually referred to as codices are rare due to their destruction by Spanish authorities; none the less 15 preConquest documents exist and depict the people's interactions with plants as well as other elements of the physical and spiritual worlds. Along with indigenous postConquest codices, the documents generated by ecclesiastical, government, and commercial authorities provide abundant textual and pictorial records of plants that influenced the life of native people as well as that of the Spanish and mestizo population. Botanical identification of the plants is limited in certain documents due to lack of adequate descriptions and/or illustrations. None the less, certain plants can be discerned from vernacular names associated with earlier illustrations as well as their etymological analysis. As sources for ethnobotanical data, the codices of the early Viceroyalty Period were complemented by later census data, commercial and tax records, and governmental inventories of useful resources (especially food and medicinal plants). Various missionaries and travellers authorized by the Spanish crown chronicled their experiences which included occasional observations about the natural history of plants. It was not until the eighteenth and the early nineteenth century that herbarium specimens and associated botanical studies permitted taxonomic identification of many plants of ethnobotanical importance. About 3000 plant names were recorded of which almost 700 have taxonomic determinations. They were important sources of medicines, food, material sources, and ornamentals.

Keywords Iconography • Codices • Relaciones geográficas • Viceroyalty Period • Reversión

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Introduction

Ethnobotany is dedicated to the study of the interactions and relationships between plants and people over space and time. *Interactions* refer to the reciprocal impacts of one component upon the other; these are consequences of such processes as co-evolution, domestication, plant management, and ecological processes (e.g., commensalism, mutualism). *Relationships* between the plant and human components reflect correlations where cases of cause-and-effect are not obvious. Examples include such cultural endeavors as cosmology, generation and transmission of knowledge, nomenclature, classification, description, transformations, exchanges, and utilization. These interactions and relationships occur throughout time and over space. The *time* component is variable. On one hand, the chronological scale of human history from the humanoid era to the anticipated future is usually assumed. None the less, one can view time from the biological–evolutionary scale, especially when considering evolutionary changes which can vary with different evolutionary clocks of organisms or velocity of genetically fixing desired characteristic through artificial selection. Physiological time expressed as growth patterns of plants can be different from normal biological time under different management regimes to which the plants are subject to. *Space* varies with reference to the positioning of the plants relative to human perspective. Depending upon which spatial attributes are given priority, the amalgamation of unit and its delimitation can vary. The cultures with social networks and customs define areas on the earth over which people interact while geopolitical forces impose their spatial control and boundary enforcements that protect the institutional policies. Many times the lack of concordance between sociocultural and political spaces is the basis of conflicts dealing with plant resources. The biogeographic space responds to interactions of biotic and abiotic factors with the biota in the context of historical geography so that regionalization of nature is at once subliminally obvious but generates alternative representations in terms of biogeographic provinces, life zones, floristic regions, vegetation types, among other categories of classification.

The *scales* at which interactions and relationships can be perceived can differ as well. One can take a global perspective of the whole ecosystem, focus on a floristic region, vegetation zone or a gradient of ecological zones, as well as concentrate on one species, its populations, or a particular individual plant. Similarly, ethnobotanical studies can encompass the cultural context, focus on a society, as well as concentrate on a community or an individual.

Another point is important; the interactions and relationships that have been considered are those we physically perceive with our five senses. However, an appreciation of the cosmology of the others worlds that ethnobotanists explore is essential. Some people perceive other worlds through additional senses that are not developed by those outside their culture. None the less, the plants are important manifestations of other beings we cannot perceive or part of a mythical landscape or time that are not part of one's conventional world. Ethnobotanists need to be aware of the world views of others as well as our own limitations.

When conducting research, ethnobotanists need to be conscious of the scale and dimensions which we share with collaborators. Consequently, respect and reciprocity are key concepts in our research. Mutual respect, confidence, and compliance with cultural norms are the foundations that permit us to enter other people's worlds to investigate their plants. Besides generating academic products and providing perspectives for other sectors of societies, ethnobotanists should share with their collaborators the perspective we have developed by working in their plant world, a form of "reversion" or reciprocity of knowledge of mutual benefit. Information and programs with value added (even if it is from outside their perspective) can be offered (not imposed) to those who have shared part of their lives and life ways.

Here we will sample this web of ethnobotany from the perspective of ethnohistorical resources from precontact time through the Viceroyalty Period. Because of the spotty nature of the information (part of which has survived, part of which was lost, and part of which was never recorded), we focus on sources of data and examples of the application of these data in ethnobotany of Mexico.

First, we need to be aware of the purposes for which the documentation was made, the people responsible for its fabrication and control, as well as the type of medium used. *Second*, we should consider if the record and its presentation were made from an emic or etic viewpoint. *Third*, the taxonomic level of the plant identification and its level of confidence are critical to providing and ethnobotanical interpretation.

Important Ethnobotanical Sources

Because the prominence of plants in ethnohistorical documents depends on the indigenous names, the earliest documents which link native plants names to recognizable botanical species are most critical. The etymological origin of the native names [1] and the illustrations of plants depicting diagnostic morphological characters [2] are essential to the identification of plants and to connecting prehispanic sources with post conquest documents. In the of Mesoamerica, the three major information sources for Mexican plants and their importance to the people of that time were written during first 60 years after the conquest of Mexico. Of those, two documents became available to academia community within the last 275 years. Below, each document is briefly described as to its origin, authors, contents, and importance as an ethnobotanical resource reflecting the relationships between people and plants shortly before the Spanish Conquest and during the first half century of the Viceroyalty Period. Further information (in addition to the references cited below) for the these documents (in chronological order of production) can be found in the respective bibliography cited after the titles: *Libellus de medicinalibus indorum herbis—Tratado sobre hierbas medicinales* indias [3–7], *Historia general de las cosas de Nueva* España [8–11], and *Historia natural de las plantas de Nueva* España [12–15]. Because many of the early ethnobotanical sources of the Viceroyalty Period focus on the medical applications of plants, it is worth noting that the major compilations on Mexican herbolaria make reference to these critical sources [16–18].

A prominent Mexican academic leader who interpreted and provided accessible to the latter two documents and their associated material was Francisco del Paso y Troncoso. During his residence in Europe between 1892 and 1916, he searched for documents related to Mexican history. Being that his professional thesis dealt with history of medicine in Mexico and was based largely upon the writings of Francisco Hernández, he was especially sensitive to references that shed light on the botanical studies of the past. Of the hundreds of published reports on documents relating to Mexican history, over 80 of his articles are of botanical interest.[1]

Libellus de medicinalibus indorum herbis—Tratado sobre hierbas medicinales indias is the first book produced in the New World dealing with American curative plants and written by indigenous people. This *Libellus* documents the encounter of native Mesoamerican remedies with European medicine. Martín de la Cruz [late XIV c.-?], an indigenous healer of fame, *ticitl*, from Santiago, Tlatelolco, had won the confidence of the viceroy of New Spain, Antonio de Mendoza, and his son, Francisco de Mendoza, who promoted de la Cruz to redact a text of local remedies. An older man without institutional schooling, he dictated examples of illness and their cures from the indigenous perspective, which was probably recorded in his native language, Nahuatl. Juan Badiano [1484–1560], a younger man from Xochimilco with knowledge of traditional medicine as well as formal education in Latin and Spanish, collaborated with the former in translating the information into Latin as well as probably adjusted the organization and terminology of parts of the document so as to be comprehensible to Spanish readers. Native artists, *tlacuilo*, painted figures of the plants, although it is unknown if they drew the illustrations from plant samples or rendered the illustrations from verbal descriptions.

Libellus was created for a practical reason and was directed to the Spanish crown. The College of Santa Cruz in Tlaltelolco near Mexico City, headed by Friar Jacobo de Grado, was facing financial decline and health crisis in this institution that was established to educate the children of the Mexican society's nobility after the Conquest of Mexico. Diseases (especially smallpox upon first contact with the Spaniards and later during 1545–1548) had reduced the indigenous population and threatened the students; also, the new college was in need of proper maintenance. These necessities required greater funding from the Spanish authorities. Upon its completion in July of 1552, Francisco de Mendoza (son of Viceroy of New Spain, Antonio de Mendoza) personally presented it to the Spanish crown as evidence of the high intellectual level of its subjects in New Spain. Also, the son the viceroy of New Spain sought to obtain crown-sanctioned concessions to commercialize American medicinal herbs; Nicolás Monardes of Sevilla profited from this venture as seen by his later importation of herbal remedies and by the publication *Historia medicinal de las cosas que se traen de nuestras Indias Occidentales*.

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[1] See I.K. Langman. A Selected Guide to the Literature on the Flowering Plants of Mexico. 1964; Philadelphia, PA: University of Pennsylvania Press. pp. 567-569.

The document was produced at College of Santa Cruz located Tlaltelolco where the students of noble background were instructed in Latin, Greek, and Spanish, learned to write their native tongue, and were evangelized. The school also served as a center to document the Mexican culture, although the authorities later censored the products. In addition to generating *Libellus*, Tlaltelolco was home to other scholars such as friar Bernardino de Sahagún who began in 1555 to generate manuscripts that later formed what is known today as the Florentine Codex o *Historia General de las Cosas de Nueva España*.

Even though King Carlos V did not examine the *Libellus*, his son who later became King Philip II of Spain probably saw it. *Libellus* remained in the royal library at Escorial; during the early seventeenth century, Diego de Cortavila y Sanabria (pharmacist of Spanish King Philip IV) incorporated it into his collection. Probably during his visit to Spain 1624–1625, Cardinal Francesco Barberini acquired the book which was catalogued as "Codex Barberini Latin 241". At that time *Libellus* drew the attention of a member of the Cardinal's staff, Cassiano dal Pozzo who made a copy which became part of the English King George III library in Windsor Castle [19]. Up to the twentieth century, the inaccessibility of the document and absence of recognized botanical names (most of which are in Nahuatl) account for the limited contribution *Libellus* made to science and medicine.

The appreciation of *Libellus* began to change in 1902 when the Barberini library was transferred to the Vatican Library in Rome. Charles Upson Clark rediscovered the book in the Vatican Library in 1929. Two scholars in particular, William Gates [3] and Emily Walcott Emmart Trueblood [4], independently studied photographs of *Libellus* and published the Latin texts with English translations along with illustrations. A Spanish version with selected drawings was published by Francisco Guerra [5]. Not until 1964, did a full color facsimile edition with Spanish translations and scientific analysis become available [6]. In 1990 during this visit to Mexico, Pope John Paul II arranged for the transfer of *Libellus* from Vatican City to Mexico where it is currently deposited in the library of the Museo Nacional de Antropologia e Historia.

The information in *Libellus* is organized by sicknesses in 13 chapters. Indigenous medical system arranges the illnesses from the head to the feet, also common order in European texts, as well as dealing with death. The relationships of some ailments are associated with cosmology of the Mexico. In other cases, European terms are used to describe specific maladies recorded in classic medical texts of the Old World such as those of Plinio, Dioscórides, and Galeno. Hence, *Libellus* documents the mestization of Mexico's medical tradition based upon indigenous concepts tempered with European influence. This mingling has created a challenge for today's researchers to not only separate the respective bases of health concepts and practices but also to identify the sources of contemporary Mexican cultural identity.

The structure of each entry in *Libellus* contrast with that of the European herbals which focused on the plants and their curative properties. But in appearance they are similar because each illness treated in *Códice de la Cruz-Badiano* is prefaced by an image of some (but not all) the plants mentioned in the corresponding remedy along with its Nahuatl name. Few plants are referred to by Latin names; such a situation may explain why the *Libellus* was not readily accepted by the medical profession of the Old World who did not recognize such foreign terms. The illustrations reflect the pre-Hispanic style with glyphs. The base of each plant is imbedded in a figure with various colors which depicts specific properties of the plant, in most cases its ecological habitat. Such holistic representation disappeared in later registers of the same century; they appear rarely in the works Sahagún and Hernández produced shortly after the *Libellus*.

The de la Cruz-Badiano manuscript illustrates 185 plants and mentions 227 plant names, mostly in Nahuatl. Since the 1930s, various scholars, principally from USA and Mexico, have proposed the taxonomic identifications of more than half of the plants based principally upon vegetal and reproductive characters in the illustrations, along with their indigenous names (some of which continue to be employed in Mexico), and its implied bioactivity derived from its medicinal application. The landmark botanical study was established by Miranda and Valdés [20] and subsequent modifications have been proposed by among others Valdés, Flores, and Ochoterena [21], Clayton and de Ávila [19] and Bye and Linares [22].

Historia general de las cosas de Nueva España (also known as the Florentine Codex) is the principal contribution of the Franciscan Friar Bernardino de Sahagún [1499–1590], today recognized as the Father of American Ethnography. Upon his arrival in Mexico in 1529 he immersed himself in the task of evangelizing the recently conquered Mexican nation. Based on the various ecclesiastical sites at the Valley of Mexico, he learned the Nahuatl language. In contrast to his contemporaries who later produced bilingual dictionaries [23], Sahagún attempted to depict in words and illustrations the cultural basis of the language. The description and explanation of pre-Hispanic religion, beliefs, practices, deities, and elements of the environment were initially intended to assist the friars and civil authorities comprehend the idolatrous religion and, in turn, convert the Aztecs to Catholicism. Over time, Sahagún appreciated the richness and value of the great cultural inheritance of the indigenous people of New Spain and attempted to record it for posterity. Certain authorities of the viceroyalty recognized that his contributions could be counterproductive and subject to an Inquisition inquiry, a situation that lead to the confiscation of his works that were sent to Spain in 1577 (known as the *Codices matritenses*) and, in 1580, the deposition of the bilingual, illustrated compilation known today as the Florentine Codex by friar Rodrigo de Sequera, the Franciscan Commissary General and Sahagún's defender. To this day, the curious omission of the Spanish translation of certain Nahuatl texts (e.g., those related to hallucinogenic plants) may be interpreted as a form of protecting indigenous knowledge or may have permitted more space of illustrations of these ethnobotanical important plants. The Archivo General de la Nación produced the first facsimile that appeared in 1979 [24]. Presently, the only full translation of the Nahuatl text is in English edition [25].

Most of the preliminary work was conducted by Sahagún at the College of Santa Cruz in Tlatelolco, near Mexico City. He was assisted by two important indigenous people: the elders of central Mexico and the Nahuatl students (and former students). The elders' responses to Sahagún's questionnaires [26] were recorded in traditional pictorial form by *tlacuilo* and the students provided interpretations and clarifications written in Nahuatl and Latin. Sahagún reviewed the Nahuatl text which he translated into Spanish. Although the compilation of information began during the 1530s, the actual compilation of the bilingual version occurred between 1575 and 1577. A possibly earlier Spanish version of 1532, is known as the *Manuscrito de Tolosa*, was deposited in the Franciscan convent of Navarra, Spain; this document may have been consulted by other earlier chroniclers of Mexico such as Francisco Javier Clavijero [27]. The original Florentine Codex consisted of 12 books (now bound in three volumes) was initially sent to Pope Gregory XIII in 1580 and later deposited in *Biblioteca Medicea Laurenciana* in Florence, Italy, where it resides today. Usually each page consists of two columns with the left column in Spanish and the right in Nahuatl. Many of the almost 2500 illustrations are in the Nahuatl column and depict people, animals, and plants with diagnostic characters in European style although a few images include pre-Hispanic artistic traits. Although plants and their relationships with people, mostly the Aztecs, are found in all 12 books, Book 11 entitled “Earthly Things, about properties of animals, birds, fish, trees, herbs, flowers, metals, and stones, and about colors” concentrates on 74 % of the plants with ethnobotanical information.

The first notice about the Florentine Codex appeared in the inventory of books in the Medici Library in 1793. In 1829–1830, Carlos María Bustamante published the Spanish texts in the first edition in Mexico with taxonomic identification of the plants by Vicente Cervantes, the Spanish botanist who arrived with the Royal Botanical Expedition during the previous century. The pictorial elements were copied between 1905 and 1907 under the supervision of Francisco del Paso y Troncoso to produce the first set of colored illustrations that were copied from the Codex and reproduced in 158 plates that have been used in most of the publications to date. The landmark reference for the botanical identification of the plants, principally in Book 11, was published in 1941 [28] while the extensive compilation of the indigenous plant names, for which 382 species have been determined, was prepared based upon the 1979 facsimile by Estrada [29].

Historia natural de las plantas de Nueva España by Francisco Hernández [1514–1587] was the first formal inventory of biotic resources of New Spain sanctioned by the Spanish Crown. In 1567, Hernandez became the court physician of King Philip II who, in 1570, charged him to document the natural history of his lands in the New World. His title “Protomédico general de nuestras Indias, islas y tierra firme del Mar Océano” (Chief medical officer of Spanish Indies, islands and lands of the Sea) covered a large area of the Spanish Empire, in particular the Caribbean Islands, contemporary Mexico and Central America to northwestern South America. Most of his time between 1571 and 1577 was spent in New Spain although his initial arrival in the New World was spent in the Caribbean region. Hernández travelled throughout central Mexico with his team that included his son as well as indigenous specialists and artists. The inhabitants bestowed upon him the name “El preguntador del Rey” (The King’s questioner) because he inquired about plants, animals, and minerals throughout the Viceroyalty as well as documented all with texts (in Spanish, some in Nahuatl), dried specimens, seeds, live plants, and drawings.

He recorded the plants by providing indigenous names (and their etymology in some cases), comparative morphological descriptions, ecological, and geographical data as well as organoleptic and pharmacological properties. Although some of the organoleptic and medicinal properties are derived from indigenous informants, the therapeutical properties reflect Galenic principles of medicine, suggesting that his work reflects more an etic perspective. While visiting convents and hospitals, he was able to record experimental results of the application of some of the remedies. In some cases he included forms of preparation and dosages in addition to their medical uses. In some cases, he presented different plants with similar names, therapeutic properties, and medical uses suggestive of the concept of medicinal plant complexes [30] in which different taxonomic entities have the same or similar plant names, similar uses, yet have different geographic distribution; usually each complex has a preferred signature species considered to be the most effective. A few of the surviving illustrations contain elements of the indigenous *tlacuilo* style and others with European style (possibly due to their depiction after the compilation of the work).

Before Hernandez passed away in 1587, King Philip II charged Nardi Antonio Recchi, a Neapolitan book editor, to produce an abbreviated edition of his work based upon the voluminous notebooks and drawings. Upon the Recchi's death in 1595, Federico Angelo Cesi of the Accademia dei Lincei completed the publication. The result was the Roman edition that became available in 1651 with the title *Rerum medicarum Novae Hispaniae thesaurus, seu, Plantarum animalium mineralium Mexicanorum* historia [31]. None the less, copies of Hernandez' notes were available and copied into publications of others. One of the most recognized is that of Francisco Ximénez [32], who published in the City of Mexico *Quatro libros. De la naturaleza, y virtudes de las plantas … en el uso de medicina en la Nueva España … que el doctor Francisco Hernandez escribió en lengua latina* with credits to Hernández. None the less, Juan de Barrios [33] also printed in Mexico City a treatise entitled *Verdadera medicina, cirugia y astrologia, en tres libros dividida* but does not credit Hernández. The detailed comparison of the documents of both Barrios and Hernández by López and Pardo [34] leaves no doubt that Barrios copied the Hernandez' first text, *Index medicamentorun Novae Hispaniae*. A similar case has been made for *El tesoro de medicinas para diversas enfermedades* by Gregorio López [35].

The plants, documents, and illustrations of the Hernandez' expedition were deposited in the library of the Royal Monastery of San Lorenzo de El Escorial (located about 45 km northwest of Madrid). Elements of his archive became disassociated from the main collection in order to further study the information, to prepare parts for publication, or to decorate the walls of the royal palace. Much of his archive was lost in the fire of 1671 in the El Escorial. Surviving fragments were assembled to produce the Madrid edition in 1790 known as *Opera: cum edita, tum inedita, ad autographi fidem et integritatem expressa, impensa et iussu region …* with chapters titled "Historia Natural de las Plantas de Nueva España" [36]. This work probably stimulated the Spanish Crown's Royal Botanical Expedition to New Spain and was supervised by Casimiro Gómez Ortega, first professor of botany at the Royal Botanical Garden Madrid. Isolated fragments have been associated with such favors of King Philip II as gifts of drawings to Jaime Honorato Pomar (professor of botany at the University of Valencia) that form part of the Pomar Codex said to date to 1590 [37].

These publications based upon the sixteenth-century expedition of Hernández constitute the primary source of botanical knowledge for Mexico and parts of the Caribbean over the next two centuries. Excerpts appeared in various international books: *Historia naturae* by Juan Eusebio Nieremberg [38], *Historia plantarum generalis* by John Ray [39], *A voyage to the islands Madera, Barbados, Nieves, S. Christophers and Jamaica* by Hans Sloane [40], *Histoire naturelle, générale et particulière, avec la description du Cabinet du Roy* by Georges-Louis Leclerc, better known as Comte de Buffon [41], *Historia antigua de México* by Francisco Javier Clavijero [42], among others. Hernández, himself, attempted to contextualize the biodiversity of New Spain by incorporating his observations in the New World into a translation of Pliny the Elder [13].

Most European books describing the world's flora published prior to 1753 make reference to plants in the Rome edition of Hernández. The basis of the attribution of any particular plant of Hernández to more recent plant species is uncertain; the synonymy may have been based upon the indigenous name, the description, or the illustration. After 1753 when Carl Linnaeus' *Species Planatarum* was published (and later recognized as the official date for priority of scientific names), some botanical treatments include names of Hernández but usually cite the synonymy in earlier publications. Linnaeus honored Francisco Hernández for his contribution to Mexican botany by dedicating to him the genus *Hernandia*,[2] of the family Hernandiaceae, with 25 species distributed in the tropics worldwide; five species are native to Mexico.

In order to re-evaluate the works of Hernández, King Charles III inaugurated the Royal Botanical Expedition to New Spain that functioned from 1787 to 1803 in direct contact with the Royal Botanical Garden Madrid. The expedition's focus was to update the two-century-old contributions of Hernández and validate the medicinal use of plants based on concepts of that period.

The most complete work of Francisco Hernández was produced by the Comisión Editora de las Obras de Francisco Hernández that was centered at the Universidad Nacional Autónoma de México between 1950 and 1984. The seven volumes include *Historia natural de Nueva España* (in two volumes plus another with commentaries on the work), Hernández' work on Pliny and his own writings. The principal source for the botanical determination of the plants was compiled by Valdés and Flores [43] in which, of the 3076 descriptions, 667 species are identified. Major advancement in the botanical interpretation during the Porfiriato Period was made by researchers at the Museo Nacional and Instituto Médico Nacional (Fernando Altamirano, Francisco del Paso y Troncoso, José Ramírez, and Manuel Urbina).

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[2] Linnaeus accepted this generic name that was originally proposed by Charles Plumier and Joseph Pitton de Tournefort in 1703 in their description of plants of the West Indies, *Nova plantarum americanarum genera*.

Other scientific institutions have concentrated on the study of the contributions of Francisco Hernández such as the Smithsonian Institution during the early twentieth century (William Safford, Paul C. Standley), University of Valencia (José María López Piñero, José Pardo Tomás), and Stanford University Press (Chabran, Chamberlin, and Varey).

Iconography

The pre-Hispanic Mesoamerican cultures have left an iconographic legacy of their cosmology and accomplishments through vibrant murals and detailed decorative artifacts distributed throughout central and southern Mexico and northern Central America. The large-scale paintings incorporated into the building's architecture provided a visual record of the rulers' accomplishments as well as served to communicate social and political values in private and public places. With the Conquest by the Spaniards, the evangelistic authorities appropriated this medium to transmit the European Catholic faith among the newly converted with historical and religious themes.

The most comprehensive project to document and interpret pre-Hispanic Mesoamerican murals is being undertaken by an interdisciplinary team centered at the Instituto de Investigaciones Estéticas at UNAM. Six areas have been designated (Cacaxtla, Teotihuacán, Área maya, Oaxaca, Costa del Golfo, and Altiplano Central) and publication of the results is underway [44–46]. Special attention has been given to the iconographic representation of the plants [2]. Plants in the murals are frequently associated with paradise and serves as metaphors for song, poetry, authority, sun, transformation, and battle [47].

For centuries, anthropological, historical, and artistic perceptions have been given to the interpretation of pre-Hispanic iconography. With recent interdisciplinary studies, alternative analyses of Mesoamerican iconography have evolved. Such is the case of the epigraphic and iconographic reinterpretation of Classic and post-Classic images of the Mayan serpent, *chan* or *kan*, and the water lily [48]. The revelation of the symbolic permutations of the water lily and the feathered serpent provides a different perspective of the Maya's cosmological watery underworld for which these mythological beings served as a conduit. The psychotropic properties of the vegetative manifestation of the mythological water lily support previous hypotheses of the ritual importance of *Nymphaea ampla* among the Mayan dynasty.

Murals of the Viceroyalty Period reflected, in general, religious themes that were important for converting the native population and providing a contemplative atmosphere for the religious community [49]. However, the recent restoration of the Augustine monastery San Cristóbal or El Divino Salvador (founded in 1540) in Malinalco, State of Mexico, has afforded ethnobotanists a rare opportunity to view plants and animals in an enchanting garden setting [50, 51]. More than 33 taxonomical identified plants are illustrated, of which 31 are medicinal. Of those, 90 % are native taxa; 77 % of these are still employed in Mexican *herbolaria* today [52]. Some of the species no longer used had indigenous religious significance.

Codices

The codices (codex, in the singular) are important Mesoamerican documents because they provide the revelatory instrument for interpreting indigenous knowledge which underwent acculturation and for permitting ethnobotanical studies from both emic and etic perspectives. They were fabricated originally from paper (derived from *amatl* (or amate, tree bark of various species, in particular *Ficus petiolaris*), *ixtli* (maguey fiber from different species of *Agave*), or *amoxtli* (an aquatic moss of unknown source)) or from animal skins (*ehuatl*). *Amatl* is the term applied to paper in Nahuatl while *huun* is the name in Maya. The physical document of collective memory is referred to as *amoxtli*, a sort of book that was doubled usually in a multiple page Z-fold or in half, third, or quarter French fold (but not as a book being bound along one side of the pages to form a single spine). Initially the Spanish military and ecclesiastical authorities feared that the natives would return to paganism and, consequently, destroyed most of the codices produced in central Mexico and Mayas. Today only 15 *amoxtli* of the precontact period are known. None the less, the Spanish authorities realized the importance of this medium of communication and appropriated the pictorial form to record information of the newly conquered lands and to proselytize the Catholic faith among the Mesoamerican people. Francisco Antonio de Lorenzana, Archbishop of Mexico, marveled at the *Matrícula de tributos* and stated that it was the truest testament to the opulence, grandeur, and majesty of the Mexican Empire. The Mesoamerican codices have attracted the attention of the authorities, the public as well as academics for almost five centuries. They dominate the Mexico's ethnohistorical foundation having been studied from various perspectives [27] and have been replicated as facsimiles (e.g., La Colección Códices Mexicanos of the Fondo de Cultura Económica) and in collections (e.g., Edición Especial Arqueología Mexicana—Series Códices) by various publishers. None the less, the leading expert on Mexican codices, Miguel León-Portilla [53] in his book overviewing the current status of codices studies and their inventories summarizes the current academic state of affairs succinctly, only an "invitación más que conclusión" (an invitation rather than a conclusion).

The pre-Hispanic codices have a purely emic viewpoint with only pictorial images, no texts. The contents focus on history (recording events and genealogies of important figures) and cosmology (registering religious calendars, rituals, and time markers). Four major codex groups are recognized: Maya, Borgia, Mexico, and Mixteco. These documents were dictated by the priests and indigenous sages (*tlamatinime*) to the recorders or painters (*tlacuilo*) who specialized in the production and reproduction of these documents on vegetal or animal parchment. The communication arising from codices required the collective memory of the privileged class. The pictorial codification in the image allowed the knowledgeable interpreters to bring the images to life through their oratory talents—"dar a luz verbal a la imagen" (to give voice to the image) [54]. The codices were sacred and the source of the society's collective knowledge, calendric events, and moral foundation. In order to prevent religious reversion and bellicose hostilities, the *amoxcalli* or indigenous libraries and their contents were destroyed. Today most of the surviving *amoxtli* are housed in foreign repositories to which they migrated over the last five centuries.

The sacredness of plants and their integration into the spiritual world as well as the natural environment are exemplified by the pillars of the cosmos in the Fejérváry-Mayer Codex [55]. The first sheet of this member of Borgia Codex group (originating probably from the Oaxaca-Puebla region) illustrates the four sacred trees supporting the four cardinal directions of the universe: the cacao (*Theobroma cacao*), a cauliflorous tree with pendent fruits, upholds the South, the turquoise-green riparian *ahuehuete* (*Taxodium mucronatum*) with woody projections or water glyphs is located in the East, the *pochote* (*Ceiba* sp.) with the spine-like bark prickles and hollow-like trunk fixes the North, and the mesquite/*huizache* (*Prosopis* sp./*Acacia* sp.) with bicolored spinose stipule spines supports the West.

Given the lack of texts, the Spanish authorities were unable to confidently read and comprehend the contents of the codices. Afterwards, they regretted the loss of long-standing records to such valuable information as the location of pueblos, communication routes, distribution of the natural resources, and access to new areas for spiritual and tactical conquest. As a consequence, the talents of the artists-recorders were revived and redirected to producing new documents in service of the civil, military, and church authorities. These *tlacuilo* (some having learned European pictorial techniques and alphabetized writing of Spanish, Latin, and Nahuatl) copied the remnants of the original *amoxtli*, repainted from memory vanished documents, and codified religious themes so as to aid the conversion of the people and uncover concealed pagan idolatry. Today over 500 codices of the Viceroyalty Period have been inventoried. The new images were labeled and transcribed into texts for interpretation. Although the content was based upon the emic perspective, the interpretation and application now contained etic viewpoints. Overtime, certain symbols changed their significances or became meaningless. The details of others degenerated and disappeared. For instance, the tree, a vital event marker in the pre-Hispanic times, acquired a hybridized appearance with a European crown and indigenous roots in the post-Conquest codices. The barrel cactus and mesquite tree that were closely linked to certain ancestral rituals shifted to decorative generalities. Curiously, the representation of the maguey diverged. On one hand, such ritual functions as the sacred refuge of *ltzpapalotl*, goddess of the ancestors, disappeared while the utilitarian functions of maguey and its management to generate the life-sustaining liquid, *agua miel* and its fermented product *pulque*, persisted in codices and were important scenes in the landscape paintings up to the twentieth century.

The Mendoza Codex and its predecessor, *Matrícula de Tributos*, registers hundreds of products paid as taxes in kind to the Triple Alliance from about 38 pueblos. Among the ethnobotanically important botanical themes illustrated are: food plants (amaranth, avocado, beans, black cherry, cacao, chia, chili, chirimoya, cuajilote, guaje, huazontle, Spanish bayonet, maguey, maize, mamey, squash, sweet potato, tuna fruit); medicinal and stimulating herbs (thistle, lobelia, tobacco); plant sources of dyes (añil, cochinilla); plant sources of materials (amate, amole, cane grass, cattails, cotton, Spanish bayonet, palm, tree gourd, willow); resin sources (amber, copal, liquidambar); and trees (bombax, oaks, pine).

New Spain's first Viceroy, Antonio de Mendoza, commissioned the Mendoza Codex between 1541 and 1542 as a gift to King Charles V in order to illustrate the rich resources from different ecological sectors of the New Spain. Unfortunately, it was captured by French pirates aboard a Spanish galleon and eventually was acquired by an Englishman who deposited it in London where it resides today. The representation of people and products with the distinctive illustrations each accompanied by the corresponding textual descriptions has permitted scholars since the sixteenth century interprets the legacy of Mexican codices. The iconographic features of the phytomorphs expressed in the pre-Hispanic style provide a link between the traditional representations of the *tlacuilo* and the later Mexican–European plant illustrations in such essential ethnobotanical works as the Florentine Codex.

Many codices include glyphs which function as ideographic location markers that have given rise to contemporary toponyms. These are important sources for ethnohistorical studies that focus not only on place names (where there are human settlements) but also geographic features in the landscape. They also provide perspectives to time depths and on ethnic affiliations [56].

An example of an ethnobotanical study of a pre-Hispanic-like codex (with traditional pictorial symbols, produced with indigenous prigments on amate paper, and without European text) is Mapa Cuauhtinchan number 2 (MC2) [57]. Almost 150 phytomorphs are presented as part of toponymic glyphs or as interactions among people and their environment. A diachronic analysis of 30 phytomorphs between the MC2's mythological age in Aridoamerica and the map's contemporary period in Mesoamerica suggests continuities as well as changes in the relationships between the plants and the Cuauhtinchan culture over time [58]. Plants such as *Agave*, *Laelia,* and *Yucca* present a symmetric association being culturally important for both periods. Other plants such as *Amaranthus*, *Capsicum*, *Leucaena,* and *Phaseolus* are part of the asymmetric pattern in that the migrating people adopted new plants upon arrival in Mesoamerica. The curious presence of *Zea mays* in the pre-Mesoamerican timeframe appears to be a contradiction. However, the facts that the figured Chichimecan person apparently harvested the plant from a sandy bank along a stream,[3] that the cane was of prime value, and that Tolteca-Chichimeca tradition required that one must eat maize before one can learn to speak Nahuatl all suggest a harmonious relationship during cultural evolution rather than an inconsistency.

Perhaps the most studied postConquest codex and one of the three key ethnohistorical documents that are critical for ethnobotanical studies is Florentine Codex. A brief description of this classic document and selected publications that provide access to botanical information are discussed above.

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[3] Sandy stream sides were common habitat used to grow (but not cultivate) maize by nonagriculturist hunters and gatherers up to the nineteenth century in America.

Relaciones Geograficas

Throughout the Viceroyalty Period, the Spanish Crown was interested in the inventory of its territories. On various occasions, census-like questionnaires were circulated to civil and ecclesiastical authorities for their responses [59]. The instructions for the *Relaciones Geográficas* (RG) were sent to 713 settlements; of the 191 RG returned for the period 1577–1585, 167 are known to be housed in Archivo General de Indias (Seville, Spain), Real Academia de la Historia (Madrid, Spain), and University of Texas (Austin, USA). Another set of RG, sometimes called *Relaciones Topográficas* (RT), was gathered between 1777 and 1778 after the expulsion of the Society of Jesus from the Spanish territories. The number of questions varied from 37 to 200. The quality of the answers is highly variable because of the many human factors such as familiarity with the region, ability to communicate in the native languages, available time for obtaining data, among others. Specific details of these reports are available [27, 60]. Because the constant change of civil and ecclesiastical political units during this period, a useful guide to the geography is that of Gerhard [61].

The rediscovery of the RG in the archives of the *Consejo de Indias* prompted interest among scholars. The academic residency of Francisco del Paso y Troncoso in Europe between 1892 and 1916 allowed him to make available copies of various documents. Many of these were published; for an extensive list of the RG of potential interest for botanical studies, one should consult Langman [62]. The available RG of Mexico and Guatemala for the sixteenth century have been published [63]; even though many plants are mentioned in the texts and noted in the glossary, there is no botanical analysis.

The five questions of most interest to ethnobotanical studies are related to: (1) wild trees and their appropriateness for construction, (2) fruit trees, (3) the grains and vegetables included in the native diet, (4) the plants introduced from Spain and their response to the new lands, and (5) the plants and aromatic herbs with medicinal or toxic properties.

Probably because of the limited knowledge of the local resources by the responders to the questionnaire, there are more reports of cultivated foreign plants than registers of native useful plants. Using RG from the Rio Balsas depression, 46 crops were introduced into the area during the sixteenth century [64]. The RG records the establishment of exotic ingredients for mole, the famous mestizo sauce of Mexico, over different periods [65]. Nonetheless, some Franciscan friars provided detailed lists of the indigenous plant names and keen observations about plant management. A diachronic study of the eighteenth century RT of Chihuahua has been able to document the continuity (and in some cases the loss) of certain medicinal and edible plants among the Tarahumara and Tepehuan of Nueva Galicia Province [66, 67]. In the one of these RT, an observant friar registered how the Tarahumara manipulated the planting of introduced mustard so as to alter this annual plant's photoperiodic response to simulate a biennial herb and promote the production of edible basal leaves rather than flowers [68].

Other Sources from the Viceroyalty Period

During the Viceroyalty Period, a variety of documental sources provide ethnobotanical insights. Shipping manifests, warehouse inventories, supply requisitions, customs declarations, taxation records, still life paintings among other archival sources document in a fragmentary manner the values, movements, demands, and utilization of plant and plant products. Travellers in quest of material riches, souls, and adventures generated few publications and archival documents for Mesoamerica. The rustic routes, the lack of accommodations, and the restrictions enacted by the Spanish Crown did not favor frequent movement or exploration of extensive areas. References for botanical sciences during most of this period are limited [69]. As a consequence, the ethnohistorical sources for ethnobotanical data are inadequate.

The testimonies of the missionaries are useful for this period. As part of their need to communicate in the native languages, various published and unpublished bilingual dictionaries were constructed; many of these contain indigenous terms for plants, especially those used as food, construction, and medicine. Some friars had the opportunity to write books about their experiences.

An English Dominican friar, Thomas Gage [1597–1656], travelled through southern Mexico and Guatemala between 1625 and 1637. After returning to Europe and converting to Protestantism, he recorded his impression of these lands, their people, and general comments about useful plants [70]. Many Jesuit missionaries with academic training were keen observers of the cultures and natural history of Mesoamerica. When they were expelled from Spanish Empire in 1767 and exiled to Europe, some of them took the opportunity to record the cultural, physical, and biological landscapes that they remembered. Francisco Javier Clavijero [1731–1787], a creole from Veracruz, focused on central México and Baja California from an historical perspective [71]. Much of his ethnobotanical observations were secondary in nature, some derived from the work of Francisco Hernández. On the other hand, the Spaniard Miguel del Barco [1706–1790] documented in text and drawings the life, including plants and indigenous people, of northwestern New Spain based upon his personal experiences [72].

Some friars were able to document culturally important plants while stationed at their monasteries. Juan de Esteyneffer [1664–1716], German Jesuit who dedicated much of his life working in mission hospitals, compiled various treatments for illnesses that he encountered. The formulations include almost 300 different plants or plant derivatives and are based upon European and indigenous medical concepts [73]. It was so popular, that, after its initial publication in 1712, various editions were produced and distributed through New Spain; it was still consulted by Mexican traditional healers during the twentieth century [74].

While based in the Central Valleys of Oaxaca, Juan Caballero [1730?–1787] documented useful plants in the valley and mountains surrounding his monastery [75]. In his *Dendrología Natural y Botaneología Americana*, 55 plants were described, named and illustrated; many were medicinal, 17 were cultivated. Near the Valle of México, another priest, José Antonio de Alzate y Ramírez [1737–1799], was dedicated to science and literature. In 1772, he wrote “Memoria del uso que hacen los indios de los pipiltzintzintlis” in which he suggested that the psychotropic effect of *pipiltzintzintli*[4] was not the work of the devil but due to natural causes [76]. Among his writings that had major impact was “Memoria sobre la naturaleza, cultivo y beneficio de la grana.” The information about this commercially important carmine pigment produced by an insect (*Dactylopius coccus*) on *Opuntia* was so valuable and the illustrations so detailed that various editions were produced in the eighteenth and nineteenth centuries [77].

A Spanish friar, Juan Navarro [1730?–1787?], contributed to the register of the plants in the area of Queretaro while living in the Franciscan monastery. Only the fifth volume of his *Jardín Americano* (dated 1801) survives today. It contains colored illustration of 517 plants, mostly native species for which he provides Spanish and native names, where possible, along with information on their application, usually medicinal [78]. He may have been stimulated to produce this work by his contacts with the Royal Botanical Expedition but probably was not acquainted with the work of Francisco Hernández.

At the end of the Viceroyalty Period, botanical documentation gained a solid footing due to the decrees of Charles III and Charles IV. The Spanish Age of Enlightenment attempted to base, in part, the development of the Spanish Empire upon science. The natural resource explorations of New Spain were carried out essentially by three groups. Under Charles III, the Malaspina Expedition [1789–1794] circumnavigated the world under the command of Alejandro Malaspina [1754–1810]. During 1791–1792, his botanical team, Tadeo Haenke, Luis Née, and Antonio Pineda explored the western coast of New Spain. They radiated from Acapulco and collected many herbarium specimens that attended to their primary interest in the flora.

The second team, Royal Botanical Expedition of 1787–1803 (also known as the Sessé and Mociño Expedition), had a more ambitious task and covered New Spain from the northwest portion to Central America. Not only did they document the flora with herbarium specimens (now deposited in Madrid) but also colored paintings (which had been lost until recently and now published) [79]. Team consisted of Martín de Sessé y Lacasta [1751–1808], Vicente Cervantes [1755–1829], Juan Diego del Castillo [1744–1793], and José Longinos Martínez [1777–1802]; afterwards, a creole graduate of the University’s botany program joined, José Mariano Mociño y Losada [1757–1820]. The major part of botanical work was published by the Royal Botanical Gardens Madrid under the authorship of its directors, Casimiro Gómez Ortega [1741–1818] and Antonio José Cavanilles [1745–1804]. Part of the team’s responsibility was to update the two-century-old work of Francisco Hernández. With the deterioration of the Spanish government in the early 1800s, much of the work was not completed. Sessé and Mociño returned to Spain with specimens and illustrations in order to publish the results. They were unable to do so before their deaths. Part of the material was dispersed among botanists in different European herbaria; part was lost. Their actual publication of Mexican flora

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[4] He compared the plant to *cáñamo*, generally referable to *Cannabis sativa*, although some authors have suggested that it is *Salvia divinorum*, *Ipomoea* sp., or *Turbina corymbosa*.

was produced at the end of the nineteenth century [80, 81]. Some plants described in the publications (of Sessé and Mociño, but not those of Gómez Ortega and Cavanilles) and drawn in the field have names written in Nahuatl, sometimes with references to Hernández. In *Anales de Historia Natural* of Madrid, these botanist and their students described only the medicinal plants that demonstrated curative effects in their experiments and clinical trials; there was no place for reporting on indigenous "superstitions" about plants that did not pass their tests. Hence, the magnificent Spanish scientific expedition that documented Mexico's flora just prior to Mexico's Independence provided limited contribution to our knowledge of the Mexico's vegetal resources and their importance to its inhabitants.

Observations recorded by non-Spanish explorers are very limited, essentially because foreigners, with one exception, were not permitted to explore the region much less take specimens and data back with them. An unauthorized opportunity to document useful plants of Veracruz occurred in 1729. A ship of the British South Sea Company was anchored in the port of Veracruz, a practice known as *asiento inglés* that allowed safe anchorage for English ships in Spanish harbors but without permission to disembark. As the ship's medical officer, William Houstoun [1695–1733] acquired (probably through the trade of contraband and the salvage of vegetal supplies brought aboard) various useful plants. These were shipped to Philip Miller [1691–1771] of Chelsea Physic Garden of London where they were grown out and described in his *Gardeners' Dictionary* [82]. Miller commented on the history, qualities, and utilities of such plants as avocado, contrahierba, jalapa, stramonia, tobacco, tomato among other important Mesoamerican plants, no doubt based, in part, on notices from Houstoun. The herbarium specimens presented to Joseph Banks for identification included those of cultural importance such as Francisco Hernández' plant *xiloxochitl flores capillaces* (as *Pachira aquatica*).

The only authorized foreign scientific expedition to the Spanish Empire in the Americas was that of Alexander von Humboldt and Aimé Bonpland. With the permission of Charles IV, they explored the route between Acapulco and Mexico City, the mining regions in central Mexico, and the route between Mexico City and Veracruz between 1803 and 1804. Their botanical specimens, which are housed at the herbaria in Paris and Berlin, are among the earliest extant herbarium specimens from Mesoamerica and form the basis of contemporary taxonomic knowledge of the regional flora based, primarily, upon the works of Kunth [83]. After returning to Europe, Humboldt published *Ensayo político sobre el Reino de la Nueva España* in 1811 (English edition) and in 1822 (Spanish edition), a detailed report of his travels, his analysis of socioeconomic statistics of the Viceroyalty, and the condition of Mexico at that time [84]. Although the taxonomic publications and the herbarium specimens lack ethnobotanical data, his *Ensayo* contains observations about 69 taxa of economic importance to colonial Mexico of which half are native [85]. Many species were important for nourishing the mining communities throughout New Spain while a reduced number generated export income via trade. Humboldt drew attention to botanically derived foods, medicines, and raw materials as an underutilized pillar of New Spain's economy with great potential for the Crown's international commerce and as the foundation for the advancement of the social well-being of its inhabitants.

Reversión: Reciprocity and Participatory Research

As defined above, ethnobotany involves different components of the interactions and relationships between plants and people over time and space. The examples above focus on major sources used in the ethnobotanical research for the timeline of pre-European contact period through the Viceroyalty Period, prior to Mexico's independence. Space does not permit the citation of examples of the application of ethnohistorical documents to such ethnobotanical phenomena as agriculture, domestication, plant migration, continuity, acculturation, biocultural diversity, and other important topics. Nonetheless, one important feature of Mexican ethnobotany deserves a brief sampling. Reciprocity between different knowledge systems is based upon mutual respect and synergistic benefits for all participants.

One of the objectives of historical research in public institutions is to make ethnohistorical documents available to present-day society in a manner that is informative. The basis of academic programs in most Mexican institutions is tripartite: investigation, teaching, and public outreach (i.e., "difusión"). Such a framework provides an influential platform for reciprocity between different knowledge systems and for participatory research of ethnobotanical investigation based upon ethnohistorical evidence.

The market provides an entry into the world of plant–human relationships that spans centuries and affords the opportunity for participatory research, especially for addressing problems of interest to the local communities. The *tianguis* of Ozumba concentrates many local useful plants that play roles in the economic and ceremonial life of the inhabitants of the region of the volcanoes Iztaccihuatl and Popocatépetl, southeast of Mexico City [86]. In recent years our market partners brought to our attention the inaccessibility of wild populations in the National Park Izta-Popo of a mountain grass, *popotl* (*Muhlenbergia quadridentata*), used for the fabrication of *escoba de popotillo* which they sold in the past. Responding to their request and in collaboration with the stakeholders (the collectors of San Pedro Nexapa, State of Mexico, and the CONANP), a cooperative ethnobotanical project revealed that the people not only harvest the subalpine grass in a sustainable manner but that there is cultural continuity registered in pre-Hispanic codices and practiced today by the surrounding communities [87]. The Codex Fejérváry-Mayer Codex and the Borbonicus Codex as well as the Sahagún's Florentine Codex record the association of this grass broom with the Mesoamerican goddess of purification, Tlazolteotl. Ritual cleansing, seed planting, and symbolic battles associated with the *Ochpaniztli* feast revolve around *Tlazolteotl* and her *escoba de popotillo*. Today the cleansing or "sweeping" ceremonies occupy this grass broom at the landscape scale (such as the mountain veneration observances of May) as well as at the domestic level in wedding ceremonies and in funerary rites of removing the "sombra" (or shadow) the dwellings of the recently departed.

Combining ethnohistorical information with archeobotanical samples has particular relevance for Mexico. Although archaeological remains are fragmentary and their representativeness is skewed by factors beyond the control of ethnobotanists, the taxonomic determination of plant remains permits the elaboration of a dynamic ethnoflora for a particular site over a certain period of time. The most visited archaeological site in Mexico is that of Teotihuacan, which flourished between 0 and 750 AC. Combining the archeoethnobotanical interpretation of such material with historical documents permits the construction of an Index of Cultural Importance [88]. In the case of Teotihuacan, 125 plants of ethnobotanical importance were identified, of which 20 were selected as the foundation for a botanical garden so as to present to the public, a vision of the relationships between plants and humans in central Mexico almost 2000 years ago. On one hand, local traditional healers were involved in the generation of comparative information. Given that there are no known direct descendants of the Teotihuacan culture, the communities surrounding the archaeological site inherited, to a certain degree, the area's ethnobotancial legacy. Also, they continue to employ certain plants in their communal ceremonies. Also, some of these plants are applied in traditional medicinal practices that are offered to the inhabitants and tourists. On the other hand, the changes of the importance of certain plants in response to climatic fluctuations and anthropogenic factors can be incorporated into public educational programs for schools, the onsite museum and the general publications so that, with this value added information, today's society possess criteria for planning the future.

The rescue and elucidation of ethnohistorical resources provide another opportunity for ethnobotanists to collaborate in the process of *reversión*. Recently, a benefactor gifted with foresight rescued a codex produced about 1540 BC on *amate* paper, Mapa Cuauhtinchán number 2 (MC2) [57]. It is one of the most pictorially expressive codices of the Tolteca-Chichimeca tradition with 147 phytomorphs and is a copy of a pre-Hispanic document destroyed during Conquest. An interdisciplinary group of scholars studied MC2 for 5 years; some of its members visited the pivotal locality, Cuauhtinchán, Puebla, and worked with inhabitants to interpret certain pictorial elements. The ethnobotanical interpretation focused on identification of the plants and selected ethnobotanical processes represented as well as on a diachronic analysis of 30 plants in mythological period and the map's contemporary time [58]. Subsequently, continuity (*sensu* Kubler) [89] was evaluated based upon the present-day field work. The images of the original document and the derived interpretation are available in two forms. The collective information is available in a book with Spanish texts. The artifact and the associated academic information are most appropriately exhibited at Puebla's regional museum, Museo Amparo, in the city of Puebla [90], because MC2 covers geographic areas bounded by the states of Mexico, Tlaxcala, Veracruz, and Oaxaca.

The application of ethnobotanical historical studies to contemporary socioeconomic circumstances is exemplified by the documentary video "Los Mezcales del Occidente de Mexico y la Distilación Prehispánica" [91]. The application of the name mezcal, a distilled liquor from "hearts" of various species of *Agave*, is protected by a 1994 Mexican law on Denomination of Origin of "Mezcal". Because the original regulation did not adequately cover the mezcal producing areas, it was modified in 2012. None the less, these laws were founded upon industrial interests rather than ethnohistorical facts. The "Mezcales…" video combines archeobotanical discoveries, data from seventeenth-century tax records, geographic distribution of toponyms, and contemporary field investigation to demonstrate that the region around the Volcano of Colima (currently excluded from the geographic denomination of origin), the region that may be the center of origin of distilled agave spirits as far back as 3500 years. The post-contact introduction of more efficient Philippine and Arabian distillation apparatus probably displaced the Mesoamerican device. The 20 ethnotaxa of mescal agaves may be in danger of disappearance if the local mescal production is repressed due to irrational application of federal regulations. Should the current legal contradiction (which presumably protects a national product, its prime material, processes, and producers) be rectified, it would illustrate the impact that reciprocity of the historical ethnobotanical research can have on the conservation of plant diversity and the fortification of national identity.

Conclusion

Interactions and relationships between humans and plants in Mesoamerica have varied over time and space. The ethnohistorical documents for the epoch between the late PreConquest period (prior to 1519) through Viceroyalty era (early nineteenth century) provide a fragmentary view. Because Mesoamerican cultures expressed their relationships with plants through glyphs and illustrations, the early Conquest documents (e.g., Codex de la Cruz-Badiano, Florentine Codex, and Natural History of Plants of New Spain) are the key for linking indigenous names and images with western scientific nomenclature.

Pre-Columbian sources such as codices and murals are limited due to the colossal destruction of indigenous codices and other cultural artifacts. The few extant items are difficult to elucidate from an emic perspective; none the less interdisciplinary studies are beginning to revise century-old etic interpretations of Mesoamerican cosmology which is strongly connected to the plant world.

PostConquest documents are based upon those generated by ecclesiastical, government, and commercial authorities. Some are products of education and communication associated with evangelization of the Catholic Church. Others include codices, census data, commercial and tax records, inventories of useful (usually medicinal) plants by agents of the Crown, chronicles of missionaries, among others. Few travellers have left testimonies of their observations of the environment of New Spain. During the Age of Spanish Enlightenment at the end of the Viceroyalty, observations of plant–human interactions were complemented by herbarium specimens which facilitated the proper taxonomic identification. The Spanish Crown sponsored official expeditions such as those of Malaspina and Sesse y Mocino. The only foreign exploration sanctioned by the Crown was that of Humboldt and Bonpland.

Despite the incomplete ethnobotanical record over this three century plus period, over 3000 plants were documented of which almost 700 have taxonomic determinations. Many of these were used medicinally while others have been employed as food, material sources, ornamentals, among other purposes. Plant–human interactions documented include plant domestication, while plant–human relationships are reflected in the nomenclatural etymology and classification. Much of the etic perspective has focused on the appropriation of useful plants by politically dominant sectors of the indigenous dynasties and later Viceroyalty society. Documents with an emic perspective diminished over time.

These ethnohistorical sources provide basic data for diachronic studies of biocultural diversity, resource management, continuity, acculturation, ethnotaxonomy among other topics. Synchronic studies may be limited due to incomplete inventory and complementary data. Nonetheless, ethnobotanists have the opportunity to share with the Mexican society this information on plant–human relationships with value added. Programs of reciprocity of ethnobotanical studies for indigenous people and the public via the analysis of the historical sources not only benefits the many Mesoamerican communities searching to rescue and fortify their cultural roots but also offers contemporary society alternatives to plan for the future.

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Chapter 4
Pre-Columbian Food System in West Mesoamerica

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Abstract The west of the biogeographic region Balsas-Jalisco is considered a center of agricultural origin and plant domestication in the New World; in this region, a complex agro-alimentary system could have generated as far back as the Archaic Period (10000–4400 BP). To date, we ignore the structure and evolution of the system found there by the Europeans in 1522; however, this knowledge is fundamental to understand the high cultural development of the area and to measure the changes produced by the conquest and the subsequent cultural subjugation. We compiled the dishes that could have been elaborated during the Post-Classic Period (900–1521 CE), incorporating archaeological, ethnographic, and ethnobotanical information. The results indicate that the food system in 1522 could have been structured with close to a hundred dishes elaborated with at least 75 wild plants, 19 domesticated or cultivated natives, 12 domesticated ones introduced from other regions, and 6 wild edible mushrooms. Some of these dishes included meat, obtained from at least 19 wild animals and 4 domesticated ones. Spirits possibly were among the major dishes of this time. The nucleus of the system was made up by the same species listed since the Archaic Period, produced in the *milpa* agro-ecosystem. The changes recorded in the food system and the diet, induced by the conquest and heightened in the last 60 years, could partly explain the high levels of decalcification, cholesterol, diabetes, and obesity among the human population native to the study area.

Keywords Domestication • Milpa agro-ecosystem • Pre-Columbian food system • West Mesoamerica

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Introduction

Small groups of hunter–gatherers, accompanied by dogs (*Cannis familiaris* L.) [1], with high mobility and gathering capacity, arrived to Mesoamerica between 10600 and 10000 before present (BP) from the Central Great Plains and the Southwest of North America [2, 3]. These groups gathered and ate grits, stems, and the baked bases of agave leaves (*Agave* spp.) (called "heads" or "cabezas" in Spanish), as well as fruits and seeds from mesquites (*Prosopis* spp.), nopales (*Opuntia* spp.), and oaks (*Quercus* spp.) [2, 4]. With the use of fire for hunting, they favored the establishment of grasslands, populations of invasive edible species, and incremented the harvesting of grain, seed, and fruits [5–7]. To toast, grind, and break grains and seeds, they used stoves and grindstones; to cook tubers and roots rich in starch and inulin they employed underground ovens; to transport and consume liquids they resorted to the bottle gourd (*Lagenaria siceraria* L.) [8].

The *Agave* species represented a basic source of aliment in the arid and subhumid zones from the Gila River in Arizona down to the Isthmus of Tehuantepec; humans consumed their floral peduncles, stems, and leaf bases, cooked in underground ovens [9–13]. On the Southwest of Mesoamerica, between 11000 and 9000 (BP), deciduous low forests established and a prolonged period of drought occurred that favored the spontaneous incidence of fires before the humid summer time, and in consequence also favored plant populations pre-adapted to fire [14, 15]. Between 10000 and 7000 BP, the paleoecological records indicate a high aggregation of carbon from Southwest Mesoamerica to Panama, which suggests the systematic use of fire by humans in this region; an accumulation of grass pollen of the *Zea* genus is also indicated, suggestive of the establishment of an agricultural system based on the production of maize, and on the clearing and burning of vegetation [15, 16]. Archaeobotanical data shows that towards 8900 BP food transformation was based on the grinding with stones, and that maize and squash had been domesticated in the surroundings of the Balsas River [16, 17].

During the Early Archaic (8900–7000 BP), in the westernmost part of the Balsas-Jalisco region, it was possible to structure a complex food system with native wild plants and lithic technology; such as the toasting over ashes under a stove (inside the compartment for firewood), soaking in water with ash, cooking in underground ovens, and the grinding with stones; and the plants at its core where the wild ancestors of *Zea mays* L., *Cucurbita argyrosperma* Huber, *Phaseolus* spp., *Capsicum annuum* L., *Solanum lycopersicum* L., *Physalis philadelphica* Lam., *Spondias purpurea* L., *Persea americana* Mill., *Agave* spp., and *Hyptis suaveolens* L. [18]. This food system could have been formed with at least 21 dishes, which included: maize popcorn; maize, bean and fat chia *pinoles*; *atoles* made with maize and plum *pinole*; chili *salsas*; squash *panile* and *picadillo* ("mincemeat"); agave bread and honey; fermented beverages like *bate*, *tejuino*, and *tepache*. The nutritional complementarity (carbohydrates-proteins-lipids) achieved through structuring a diet based on maize, beans, and squash could have been an incentive for the development of the *milpa* agro-ecosystem [18].

Paleobotanical records suggest that during Mid Archaic (7000–5550 BP), agriculture in the Balsas-Jalisco intensified with the use of levers and sowing canes that facilitated the extraction and elimination of tree and shrub roots, and the picking of stones out of the soil, which allowed for better rainwater capture and ventilation of the cultivated plant's root system. All of this permitted a shorting of set-aside periods, and the establishment of crops on hills and valleys [3, 15]. The archaeobotanical and molecular genetic evidence indicates that by 6300 BP, maize gave cobs with two or four rows of kernels, which had reduced glumes [19]; it also shows that the allele for a disjointed rachis in the ear had fixed by that time [20]. By 5500 BP they reveal the presence of cobs with 8 and 12 rows, and the fixing of the alleles for 4 rows of kernels, suggesting a strong human selection during harvest, grinding, and consumption [20].

During the Late Archaic (5550–4400 BP), the evidence implies that the alleles which determined the single-shaft architecture of maize had fixed [20]; this allowed the bean vines to climb into maize, and so both plants began to occupy the same habitat, in different niches [3]. The evidence also marks the fixing of those alleles involved in the quality of protein and starch in the kernel, insinuating that the food system and the *milpa* agro-ecosystem were structured simultaneously.

Circa 4400 BP ceramics appear for the first time in Mesoamerica, on the south coast of Guerrero, which were probably related to the transformation and consumption of food [21]. During the Early Formative (4400–3100 BP), a complex *corpus* of ceramics was developed in the west end of the Balsas-Jalisco region that allowed cooking in water and in vapor, soaking and cooking in water with ash and lime, and possibly the distillation of ferments [22]. During the Mid and Late Formative (3100 and 1850 BP), this area developed a food system that could have included close to 66 dishes and beverages, employing native domesticated plants and animals, and in which maize, squash, beans, and chili peppers still were the core [23].

At present, it is unknown how the food system found by the Europeans upon their arrival to the west of Mesoamerica in 1552 was structured and continued to evolve; this knowledge is fundamental to understand the high cultural development of the area and to measure the changes induced by the conquest and the following cultural subjugation. Therefore, the general objective of this study is to understand the structure of the food system of West Mesoamerica that could have been found by Europeans in 1522.

Methodology

Selection of the study area. We selected six communities from the Zapotitlan de Vadillo Municipality, Jalisco, Mexico, which is located on the western edge of the Balsas-Jalisco biogeographic region [24]. The municipality borders with three protected areas: Manantlan Biosphere Reserve (dedicated to the preservation of the wild relatives that gave rise to maize), the Colima Volcanoes National Park, and the private ecological reserve "El Jabalí" (Fig. 4.1). We selected these communities

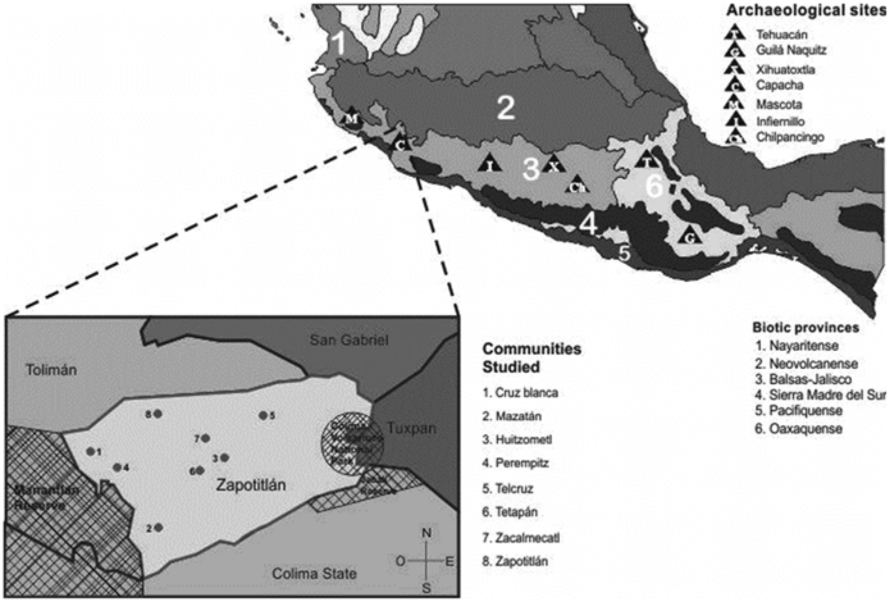

Fig. 4.1 Studied area and communities in west Mesoamerica. Map modified from [24]

because some of their farmers still cultivate with ancient methods; abiding by the *milpa* agro-ecosystem, associating maize, beans, and squashes; employing fire as a method to clear natural vegetation; using the wooden cane to sow and the wooden hoe to turn the soil and to weed, with human energy. This composition is an agro-ecosystem known locally as *coamil*.

Compilation of the archaeological information. We inspected the archaeological records concerning lithic and ceramic food technology, reported for the Post-Classic Period (900–1521) in Christian Era (CE). Furthermore, we revised the ritual ceramic records that depicted flora and fauna relevant as food, beverages, or clothing [25–37].

Compilation of the ethnographic information. We reviewed and recorded ethnographic information of the Early Colonial Period (1522–1580 CE), about native plants and animals that were employed in food elaboration. We included the *Relación Sumaria de Visitas* (1551–1554) [38] and the *Relaciones Histórico-Geográficas de La Nueva España y Michoacán: Alimanzin*, *Amula*, *Coalcomán*, *Motines de Colima*, *Tamazula*, *Tuspa*, *Zapotlán y Zapotitlán* [39–43].

Compilation of the ancient dishes. We compiled ancient dishes that could have been elaborated since the Pre-Columbian Period utilizing: (1) native wild plants, fungi, and animals; (2) native domesticated cultivated or raised plants and animals; (3) domesticated plants introduced before 1522; (4) lithic and ceramic tools, available during the Post-Classic Period (900–1521 CE).

The compilation was achieved by asking informants from Zapotitlan de Vadillo that remembered the *Nahua* tongue and possessed information regarding the oldest dishes from the region. These primary informants led us to new informants from neighboring communities. Based on these open interviews, we made the inventory of dishes and beverages, and we elaborated them in the same manner they use since the times of their great-great-grandparents (grandparents of their grandparents). The studied communities and the amount of informants were: Cruz Blanca (3), Huitzometl (1), Mazatan (3), Perempitz (2), Telcruz (12), Tetapan (2), Zacalmecatl (3) y Zapotitlan (14) (Fig. 4.1). The 40 informants had ages between 45 and 98, with an average of 69; 26 were females and 14 males. Specimens were herborized of both the wild and domesticated plants used for the dishes and beverages, and we noted the technology involved in their preparation. Simultaneously, we created a photographic record of the plants, cooking implements, and processes of elaboration. The botanic samples were deposited in the herbaria of the Yucatan Center for Scientific Investigation (CICY) and the University of Guadalajara Botanical Institute (IBUG). The seed samples were deposited in the Genetic Resources Bank of the University of Guadalajara and of the National Seed System (SNICS-SAGARPA).

Results

Instruments related to the food system during the Pre-Columbian Period. The archaeological records from the Post-Classic show a lithic *corpus* composed of three-stone stoves; underground ovens; grindstones, with or without legs, denominated *metates* and *huilanches*; macerating stones or mortars, with or without legs, called *molcajetes*. The records also show a ceramic *corpus* of deep plates or bowls; wide mouthed pots; pots with lids able to contain water; pitchers; bifid and trifid stirrup vessels; thin-waisted vessels of various shapes and sizes (*bules*); jars and bottles suitable for liquids; miniature cups; griddles (*comales*), and smoking pipes [28–34].

Ethnographic records of the Early Colonial Period indicate that vegetable implements were used for the elaboration, consumption, and storage of food, e.g., bindings, sieves, and nets from cotton (*Gossypium*) and *ixtle* (*Agave* spp.), drying beds, strainers, baskets, hooks, spears, arrows, and traps, all made from the stalks of *otate* (*Otatea acuminata* (Munro) C.E. Calderón & Soderstr). Furthermore, there are mentions of a wide variety of food and liquid containers, fashioned out of the fruits of *Lagenaria siceraria* (Molina) Standl. and *Crescentia alata* Kunth [39–44].

Structure of the food system during the Pre-Columbian Period. We recorded that the food system could have been composed by more than 108 dishes that could be elaborated with at least 75 native wild plants, 19 domesticated or cultivated natives, 5 domesticated that were possibly introduced before the Classic, 7 domesticated species introduced before or during the Post-Classic, and 6 wild fungi species; and it also incorporated the (hunted) meat of 18 wild animals, 4 domesticated species (A*nas clypeata*, *Cannis familiaris*, *Meleagris gallovapo* y *Ortlalis poliocephala*), and the recollection honey of 2 native bee species (*Melipona* sp. y *Trigona* sp.) (Table 4.1).

Table 4.1 Ancient dishes and drinks made from wild, cultivated, or domesticated plant species in the municipality of Zapotitlan, Jalisco, Mexico, which presumably were elaborated in the Pre-Colombian period

Dishes and drinks	Cook techniques
A. Foods	
Atoles	
Chili atole	Maize kernels (*Zea mays*[a]) soaked for one night in water, grounded, diluted in water boiled with *Capsicum annuum*[a] fruits
Chocolate atole	Maize kernels (*Zea*) soaked for one night in water, grounded, and diluted in water with cacao seeds (*Theobroma cacao*[b]) and vanilla (*Vanilla planifolia*[b]) pods and boiled
Guava atole	Sun-dried *Psidium guajava*[a,c] or *P. sartorianum*[a,c] fruits soaked overnight and mashed in water, added to white atole and boiled
Hog plum atole	Sun-dried *Spondias purpurea*[a,c] fruits soaked overnight, mashed in water and boiled, added to white atole and boiled
Mojo-Mezquite	Sun-dried *Brosimum alicastrum*[c] or *Prosopis laevigata*[c] fruits soaked overnight, mashed in water and boiled, added to white atole and boiled
Ranchero atole	Tender white maize kernels boiled, grounded, and diluted in water, added with *Capsicum* fruits and *Tagetes filifolia*[c] leaves
Sour atole	Maize kernels (*Zea*) soaked for 2 or 3 days in water, grounded and diluted in water. Panile on top
White atole	Maize kernels (*Zea*) soaked for one night in water, grounded and diluted in water and boiled
Dobladas	
Squash flower	Toasted thin disks of dough alkaline boiled white maize (tortilla), folded with flower boiled pumpkins (*Cucurbita argyrosperma*[a,c]; *C. radicans*[c]; *C. pepo*[b]; *C. moschata*[b])
Quelite	Tortilla folded with quelites boiled (*Amaranthus hybridus*[c], *A. spinosus*[c], *Chenopodium berlandierii*[c], *Phytolacca* sp.[c] or *Portulaca oleracea*[c]), tomato or miltomate (*Solanum lycopersicum*[a]) or (*S.l.* var. *cerasiforme*[c]) and chili (*Capsicum*) sauce
Mushrooms	Tortilla folded with boiled mushrooms (*Agaricus campestris*[d])
Beans	Tortilla folded with fresh beans (*Phaseolus lunatus*[a,c]) *boiled*
Eggs	
Boiled	Turkey (*Meleagris gallopavo*), duck (*Anas clypeata*), chachalaca (*Ortalis poliocephala*), or iguana (*Iguana iguana*) eggs cooked in water
In chili sauce	Turkey (*Meleagris*), duck (*Anas*), or chachalaca (*Ortalis*) eggs cooked and mixed with tomato (*Solanum*) or tomatillo (*Physalis angulata*[c] *or Ph. philadelphica*[a,c]) sauce
En camiseta	Egg cooked turkey (*Meleagris*), duck (*Anas*), chachalaca (*Ortalis*), iguana (*Iguana*) in tortilla
Palomitas	
Corn pop	Corn grains (*Zea mays*[a]) roasted in hot ashes
Parota pop	Parota seeds (*Enterolobium cyclocarpum*[c]) roasted in hot ashes
Pinoles	

(continued)

Table 4.1 (continued)

Dishes and drinks	Cook techniques
Bean pinole	Toasted and grinded beans seeds (*Phaseolus vulgaris*[a,c]; *P. lunatus*[a,c]¸ *P. coccineus*[a,c])
Chan pinole	Toasted and grinded chan seeds (*Hyptis suaveolens*[a,c])
Corn pinole	Toasted and grinded maize grains (*Zea*)
Cucurbita pinole	Toasted and grinded squash seeds (*Cucurbita* spp.)
Guasima pinole	Toasted and grinded guazima (*Guazuma ulmifolia*[c]) dried and ground fruits
Pipianes	
Panile	*Cucurbita argyrosperma*[a,c] or *C. pepo*[b] seeds washed, toasted, grounded, and boiled
Pipian	Toasted *Cucurbita* spp. seeds grounded and boiled with salt and *Physalis* fruits
Pipian meat	Turkey (*Meleagris*), ducks (*Anas*) or (*Podilymbus podiceps*), huilota (*Zenaida macroura*) or chachalaca (*Ortalis*) meat boiled with the pipian
Pipian vegetables	*Jacaratia mexicana*[c] fruits, *Nopalea karwinskiana*[a,c], *Opuntia atropes*[c], *O. ficus-indica*[b], *O. fuliginosa*[c], or O. *puberula*[c] sliced stems, or *Cucurbita ficifolia*[b] fruits boiled with the pipian
Pozole and birria	
Pozole	Nixtamalized maize grains (*Zea*) boiled, without the kernel tip, with wild boar or turkey (*Meleagris*) meats. Tomato (*Solanum*) and chili (*Capsicum*) sauce added
Pozolillo	Tender corn kernels (*Zea*) boiled with turkey (*Meleagris*) meat. Tomatillo (*Physalis*) sauce added
Birria	Deer (*Odocoileus virginianus mexicanus*) or Jabali (*Pecari tajacu*) with tomato (*Solanum*) or tomatillo (*Physalis*) sauce and orégano (*Lippia graveolens*[c]). Baked underground
Roasted	
Animals	Conejos (*Sylilagus* spp.); Iguana (*Iguana*); Tejon (*Nasua narica*); Tezmo (*Notocitellus annulatus*); Tuza (*Pappogeomys bulleri*)
Fruits o seeds	Beans (*Phaseolus coccineus*[a,c], *P. lunatus*[a,c]), Calabazas (*Cucurbita* spp.); Cacahuate (*Arachys hypogea*[b])
Tallo o palmito	*Nopalea*, *Opuntia* spp., *Otatea acuminata*[c] toasted
Roots	*Begonia barkeri*[c], *Ceiba aesculifolia*[c], *Dioscorea remotiflora*[c]
Salsas	
Chile and tomato	Fresh or dried chili (*Capsicum*) with fresh or dried tomato (*Solanum*) or tomatillo (*Physalis*)
Guacamole	*Persea americana*[a,c] fruits fresh crushed mixed with tomato (*Solanum*) sauce
Guaje sauce	Fresh guaje seeds (*Leucaena leucocephala*[c]) mixed with tomato (*Solanum*) sauce
Hog plum sauce	Crushed fresh, dry, or boiled *Spondias* fruit mixed with fresh, dried, or boiled *Capsicum* fruits
Parota sauce	Crushed dry parota (*Enterolobium*) seeds with dry *Capsicum* fruits

(continued)

Table 4.1 (continued)

Dishes and drinks	Cook techniques
Picadillo	Washed and grounded *Cucurbita* spp. fresh seeds mixed with fresh tomato (*Solanum*) sauce
Tomatillo sauce	Crushed fresh, dry, or boiled *Capsicum* fruits mixed with fresh, dried, or boiled *Physalis* fruits
Tomato sauce	Crushed fresh, dry, or boiled *Capsicum* fruits mixed with fresh, dried, or boiled *Solanum* fruits
Sopes	
Beans	Toasted thick disks of dough alkaline boiled corn (*Zea*) and grounded with boiled bean (*P*. vulgaris[a,c])
Squash flowers	Toasted thick disks of dough alkaline boiled corn (*Zea*) and grounded with boiled squash flowers (*C. argyrsperma*[a,c], *C. pepo*[b], *C. moschata*[b])
Elote sope	Thick disks of fresh corn (Zea) and grounded
Guamuchil sope	Toasted thick disks of alkaline boiled of maize white grains (*Zea*), crushed, and grounded with dry guamuchil (*Pithecelobium dulce*[c]) seeds
Parota sope	Toasted thick disks of alkaline boiled of maize white grains, crushed, and grounded with fresh parota (*Enterolobium*) seeds
Quelite sope	Toasted thick disks of alkaline boiled of maize white grains, crushed, and grounded with quelites (*A. hybridus*[c], *A. spinosus*[c], *Chenopodium*, *Phytolacca*, *or Portulaca*) fresh and boiled leaves
Soups: animals	
Catfish soup	Catfish (*Ictalurus dugesii*) meat boiled with tomato (*Solanum*) sauce
Iguana or Rana	*Iguana* o *Rana* sp. meat boiled with tomato (*Solanum*) sauce
Crab soup	Boiled crab (Crustacea: Decapoda) with tomato (*Solanum*) sauce
Shrimp soup	Boiled shrimps (*Cambarellus* sp., *Litopenaeus vannamei*; *Macrobrachim americannum*;) with tomato (*Solanum*) or tomatillo (*Physalis*) sauce
Turkey soup	Boiled turkey (*Meleagris*) meat with tomato (*Solanum*) or tomatillo (*Physalis*) sauce
Wasp soup	Boiled larvae wasp *Vespidae* (Hymenoptera) with salt
Soups: vegetables	
Beans soup	Beans (*Phaseolus vulgaris*[a]; *P. lunatus*[a]; *P. coccineus*[a]) boiled in water with salt and *Chenopodium ambrosoides*[a,c] leaves. Tomato (*Solanum*) or tomatillo (*Physalis*) sauce added
Congos soup	Mushrooms (*Volvariella bombycina*[d]; *V. volvacea*[d]; *Lactarius indigo*[d]; *Amanita* comp. *Caesaria*[d]) boiled in water with salt and Tomato (*Solanum*) or tomatillo (*Physalis*) sauce added
Cuervos soup	Beans (*P. vulgaris*[a]) boiled with *Ustilago maydis*[d]. Tomato (*Solanum*) or tomatillo (*Physalis*) sauce added
Esquites	Tender corn kernels boiled with *Chenopodium ambrosoides* leaves
Guaje soup	*Leucaena leucocephala*[a,b] leaves boiled with *Solanum* fruits
Hog plum soup	*Spondias* leaves boiled with *Solanum* fruits
Nopales soup	*Opuntia* spp. sliced stems boiled with *Solanum* or *Physalis* fruits
Parota and beans	Beans (*P. lunatus*[a,c]) boiled with *Enterolobium* dried seeds. Tomato (*Solanum*) or tomatillo (*Physalis*) sauce added

(continued)

Table 4.1 (continued)

Dishes and drinks	Cook techniques
Quelites soup	Quelite leaves (*A. hybridus*[c], *A. spinosus*[c], *Chenopodium*, *Phytolacca*, or *Portulaca*) boiled with tomato (*Solanum*) or tomatillo (*Physalis*) fruits
Squash and beans	Tender beans (*Phaseolus*) boiled with *Cucurbita* fruits. Tomato (*Solanum*) or tomatillo (*Physalis*) sauce added
White beans soup	White beans (*P. vulgaris*) boiled. Tomato (*Solanum*) or tomatillo (*Physalis*) sauce added pipian
Tamales	
Ash tamale	Dough made of grounded maize grains (*Zea*) soaked overnight in water with ashes, with a filling of boiled and grounded beans (*Phaseolus* spp.). Wrapped with fresh corn husks or wild grape (*Vitis poponoii*[c] or *V. tiliifolia*[c]) and baked in earth oven or steam boiled
Bean tamale	Dough made of grounded nixtamalized maize grains (*Zea*), with a filling of boiled and grounded beans (*Phaseolus* spp.). Wrapped with milpilla (*Zea perennis*[c]) or tamalera leaves (*Oreopanax peltatus*[c]) and baked in earth oven or steam boiled
Chili sauce tamale	Dough made of grounded nixtamalized maize grains (*Zea*), with a filling of tomato, miltomate (*Solanum*), or tomatillo (*Physalis*) sauce. Wrapped with corn cob husks and steam boiled
Egg tamale	Dough made of grounded nixtamalized maize grains (*Zea*), with a filling of boiled turkey (*Meleagris*) or iguana (*Iguana*) eggs mixed with tomato (*Solanum*) or tomatillo (*Physalis*) sauce. Wrapped with corn cob husks and steam boiled
Elote tamale	Dough made of crushed tender white maize kernels (*Zea*) crushed. Wrapped with corn cob husks and steam boiled
Hog plum tamale	Re-hydrated *Spondias* fruits, crushed and wrapped with corn cob husks
Meat tamale	Dough made of grounded nixtamalized maize grains (*Zea*), with a filling of boar (*Pecari*), turkey (*Meleagris*), deer (*Odocoileus*), armadillo (*Dasypus novemcinctus*), or iguana (*Iguana*) meat cooked and mixed with tomato (*Solanum*) or tomatillo (*Physalis*) sauce. Wrapped with corn cob husks and steam boiled
Mezcal tamale	Dough made of maize pinole sweetened (*Zea*) with Agave syrup (*Agave angustifolia*[a,c]; *A. maximiliana*[a,c]; *A. rhodacantha*[a,c]) with a filling of boiled and grounded beans (*Phaseolus* spp.). Wrapped in tamale plant leaves (*Vitis* spp.; *Tilia* sp.) and baked in earth oven
Nopal tamale	Dough made of grounded nixtamalized maize grains (*Zea*), with a filling of boiled slices of *Nopalea or Opuntia* spp. stems. Wrapped with corn cob husks and steam boiled
Parota tamale	Dough made of grounded nixtamalized maize grains (*Zea*), with a filling of boiled and grounded parota seeds (*Enterolobium*). Wrapped with corn cob husks and steam boiled
Pitaya tamale	Fresh *Stenocereus queretaroensis*[c] fruits, crushed, boiled, and wrapped with corn cobs husks

(continued)

Table 4.1 (continued)

Dishes and drinks	Cook techniques
Quelites tamale	Dough made of grounded nixtamalized maize grains (*Zea*), with a filling of quelites leaves (*Amaranthus* spp., *Chenopodium berlandierii*[c], *Phytolacca* sp. or *Portulaca*). Wrapped with corn cob husks and steam boiled
Squash tamale	Dough made of grounded nixtamalized maize grains (*Zea*), with a filling of fresh *Cucurbita* spp. flowers. Wrapped with corn cob husks and steam boiled
Tortillas	
White tortilla	Toasted thin disks of dough alkaline boiled white maize (*Zea*)
Yellow tortilla	Toasted thin disks of dough alkaline boiled Yellow maize (*Zea*)
Black tortilla	Toasted thin disks of dough alkaline boiled black maize (*Zea*)
Tostadas	
Puras	Toasted tortillas with salt
Chili	Toasted tortillas with milling chili (*Capsicum*)
Avocado	Toasted tortillas with crushed fresh avocado (*Persea*)
Tomato sauce	Toasted tortillas with crushed boiled tomato (*Solanum*) and chili (*Capsicum*)
Others	
Mezcal bread	Baked *Agave* spp. stems, sun-dried
Mezcal syrup	Boiled juice extracted from the baked Mezcal (*Agave* spp.) leaves bases
Ponteduro	Aggregation of toasted maize grains and *Cucurbita* spp. seeds, maize pinole (*Zea*), honey bee (*Melipona* sp. or *Trigona* sp.), or mezcal (*Agave* spp.) syrup
Potato and honey	Roots of *Ipomoea batatas*[b] boiled with honey bee (*Melipona* sp. or *Trigona* sp.)
B. Beverages	
Acorn tea	Sun-dried *Quercus rugosa*[c] fruits grounded, toasted, and diluted in hot water and boiled
Bate	Chan (*Hyptis*) and maize (*Zea*) pinoles diluted in water and sweetened with *Agave* spp. syrup
Horchata	Washed and grounded *Cucurbita* spp. fresh seeds, diluted in water and sweetened with *Agave* spp. syrup
Guanabana	*Annona muricata*[b] fruit diluted in water
Mojo tea	Sun-dried mojo (*Brosimum*) fruits grounded, toasted, diluted in hot water and boiled
Chocolate in water	Cacao seeds (*Theobroma*) boiled in water whith vanilla (*Vanilla*) pods
Fermented beverages	
Hog plum tepache	*Spondias* juice fermented in rock pits
Mezcal tepache	Baked *agave* (*Agave angustifolia*[a,c], *A. maximiliana*[a,c], *A. rhodacantha*[a,c]) juice fermented in rock pits
Mezquite tepache	*Prosopis* fruits fermented in water for several days

(continued)

Table 4.1 (continued)

Dishes and drinks	Cook techniques
Piña tepache	*Ananas comosus*[b] juice fermented for several days
Chucuhuixte	*Bromelia plumieri*[c] juice fermented for several days
Guámara tepache	*Bromelia pinguin*[c] juice fermented for several days
Tejuino	Maize soaked in water for 2 or 3 days, grinded, diluted in water, and sweetened with *Agave* spp. syrup
Chilacayote	*Cucurbita ficifolia*[b] fruits fermented in water for several days
Lechuguilla	Juice of *Agave maximiliana*[a,c] leaves and fermented for several days
Pulque	*Agave maximiliana*[a,c] *sap fermented*
Distilled beverages	
Chucuhuixte wine	Distilled *Bromelia plumieri*[c] fermented
Hog plum wine	Distilled *Spondias* ferment
Mezquite wine	*Prosopis* fruits fermented in water for several days
Mezcal wine	Distilled *Agave* ferment
Fresh	
Fruits	*Acantocereus ocidentallis*[c]; *Annona longiflora*[c]; *A. reticulata*[c]; *Acracomia aculeata*[c]; *Casimiroa edulis*[c]; *Celtis iguanaea*[c]; *Crataegus pubescens*[c]; *Cyrtocarpa procera*[c]; *Diospyros dygina*[b]; *Epiphyllum angulier*[c]; *Ficus obtusifolia*[c]; *F. padifolia*[c]; *Fuchiosa fulgens*[c]; *Heliocereus speciosus*[c]; *Hylocerus ocamponis*[c]; *H. pupusi*[c]; *Inga laurina*[c]; *I. vera*[c]; *Manilkara zapota*[a,c]; *Morisonia americana*[c]; *Myrciantes fragans*[c]; *Pachycerus pecten-aboriginum*[c]; *Parmentiera aculeata*[a,c]; *Pouteria sapota*[b]; *Rubus* sp.[a,c]; *Dideroxylon portoriciense*[c]; *Stenocereus fricii*[c]; *Thevetia ovata*[c]
Roots or palmito	*Pachyrisus erosus*[a,c]; *Cryosophila nana*[c]

[a] *Domesticated or cultivated plant*
[b] Introduced plant
[c] Wild plant
[d] Wild mushrooms

The principal dishes were *atoles*, popcorn and *pinoles*, *pipianes*, chili pepper salsas, steamed *tamales*, baked *tamales*, animal and vegetable soups, tortillas, *sopes*, *dobladas*, and toasted tortillas, while the most important beverages were the ferments, e.g., *tepache* (Table 4.1).

Discussion

With the vegetable, ceramic, and lithic technologies available in the Post-Classic, human groups could elaborate their food through sun drying, salt drying, toasting on ashes, roasting with fire, baking, soaking in water with ash or with lime, grinding, boiling in water or steaming, fermentation, and possibly distillation [18, 22].

The archaeological records indicate that the most important technological innovation during the Post-Classic, concerning food elaboration, was the *comal*, a ceramic griddle that allowed the cooking of nixtamalized maize dough for *tortillas*, *sopes*, *dobladas*, and *tostadas*. The combination of soaking, precooking in water with lime (nixtamalization), fresh grinding (dough), and the double cooking on *comal*, allowed to improve the quality of maize as a food source [45]. Additionally, it facilitated the elaboration of great quantities of food for the population dedicated to construction, religion, arts, or for the armies [32, 34].

The archaeological records, however, give little information concerning the flora used as food sources, since they only note maize, squashes, and two agave species (*Agave angustifolia* y *A. maximiliana*) and four fruit trees: *Annona longiflora S. Watson or A. reticulata* L.; *Diospyros digyna* Jacq.; *Pachycereus pecten-aboriginum* (Engelm.) Britton & Rose; *Stenocereus queretaroensis* (F.A.C. Weber) Buxbaum; and *Jacaratia mexicana* A. DC [22, 35, 46].

Meanwhile, the ethnographic record only mentions 30 edible plants as native or "of the land" [44]; nonetheless, 12 of them do not have wild relatives in the area: *Annanas cumosus* (L.) Merr; *Annona muricata* L.; *Arachis hipogea* L.; *Cucurbita moschata*, *C. pepo*, and *C. fiscifolia*, *Ipomoea batatas* L.; *Manihot esculenta* Crantz; *Nicotiana rustica* (L.) Opiz; *Pouteria sapota* (Jacq.) H.E. Moore & Stearn; and *Theobroma cacao* L. [44] indicating that these plants were introduced before the arrival of Europeans. Even though we could not find any reference in historical sources regarding vanilla (*Vanilla planifolia* Andrews), this species could have arrived together with cacao, as occurred elsewhere in Mesoamerica [47].

Both the archaeological and ethnographic records note, in a ceremonial context, the use of various fungi species (*Psilosibe* spp.), peyote (*Lophophora williamsii* (Lemaire ex Salm Dyck) J.M. Coulter), and of tobacco (*Nicotiana*) [44, 48]. However, we did not record the use of said species.

With regard to fauna, of the 19 animal species that we found were used in dishes, 12 are archaeologically represented [23; Table 3] and the ethnohistoric sources indicate breeding and consumption of dogs (*Cannis familiaris*), turkeys (*Meleagris gallopavo*) and of northern shovelers (*Anas clypeata*), as well as collection and consumption of the honey produced by native bees (*Melipona* sp. and *Trigona* sp.). The high economic relevance of this latter product is inferred due to its relevant role in tributes [44]. Furthermore, we noted the breeding and consumption of *Ortalis poliocephala*; yet no current consumption *Canis familiaris* could be recorded.

During the Early Colonial Period, the Europeans noted five agricultural systems in the area where the native population produced its own nourishment: (1) dryland milpa or *coamil*, established on hillsides under the slash-and-burn system; (2) permanent milpa with two harvests per year (*amapile*), established on plains irrigated by diversion channels. Both these systems produced: maize, squashes, beans, chilies, tomatoes, ground cherries, chia, and quelites; (3) the hillside or dryland orchard, established beside homes, which produced: *Agave*, *Enterolobium*, *Jacaratia*, *Leucaena*, *Opuntia*, *Pachycereus*, *Prosopis*, *Spondias*, and *Stenocereus*; (4) dryland plantations on sloped or flat terrain that could produce *ixlte* and mezcal (*magueyales*) or cotton (*algodonales*); and (5) orchards under irrigation, with diversion channels that yielded *Theobroma* and *possibly Vanilla*, associated with *Annanas*, *Annona* spp., *Diospyros*, *Manilklara*, *Persea*, and *Pouteria* [38, 39, 47, 48].

The food system that the Europeans might have found was based on maize, squashes, beans, chilies, tomatoes, ground cherries, fat chia, agaves, and avocados, and might have been constituted by four types of dishes: (1) the quotidian, e.g., white *atole*, *tamales*, tortillas and *sopes*, salsas and soups; (2) Dishes for long journeys, e.g., *pinole*, and mezcal bread and *tamales*; (3) Dishes for festivities, e.g., sour *atole*, *bate*, *tejuino*, ash, bean, and meat *tamales*, *pipian*, *birria*, red maize *pozole*, *pozolillo*, squash "mincemeat," and *tepaches*; and (4) Ceremonial or ritual dishes, e.g., popcorn, *pinole*, *tejuino*, black tortillas, red maize *pozole*, *tepaches*, and spirits. The psychotropic plants *Psilosibe* spp. and *Lophophora* are involved in the rituals [49, 50].

Nixtamalized maize represented the main source of carbohydrates, with high contents of assimilable calcium and potassium, consumed in *atoles*, *tamales*, tortillas, *sopes*, *dobladas*, and *tostadas*. This carbohydrate source was possibly complemented with underground baked agaves. The beans (*Phaseolus coccineus*, *P. lunatus*, *and P. vulgaris*) made up the main protein source, complemented by the toasted seeds of *Enterolobium cyclocarpum and Prosopis laevigata*. Squash seeds (*Cucurbita argyrosperma*; *C. fiscifolia*, *C. moschata*; *C. pepo*), together with *Hyptis*, were the principal source of lipids, complemented by avocados. The main sources of vitamins and minerals could have been chilies (*Capsicum*), tomatoes (*Physalis* spp.), ground cherries (*Solanum*), plums (*Spondias*), *guajes* (*Leucaena*), and quelites (*Amarathus*, *Chenopodium*, *Phytolaca*, and *Portulaca*).

The occasional consumption of meat in festive dishes could bolster the intake of proteins and fats; the meat was eaten roasted or cooked in water and seasoned with chili, epazote (*Chenopodium ambrosioides*), oregano (*Lippia graveolens*), plum (*Spondias*), avocado (*Persea*), guaje (*Leucaena*), or diverse salsas.

Fermented beverages like *tejuino* (*Zea-Agave*) and *tepaches* (*Agave angustifolia*, *A. maximiliana* (lechuguilla), *A. rhodacantha*; *Annanas*; *Bromelia plumieri*; *B. penguin*; *Prosopis* and *Spondias*) could have had a prominent role in the diet due to their contribution of vitamins and probiotics and were important as quotidian, festive, and ritual meals [44, 51]. Meanwhile, agave spirits could have been the main source of alcohol for festive and religious activities [50]. The juice of baked mezcal (*Agave* spp.), the honey of native bees, chocolate, and possibly vanilla could have been relevant pieces of the food system, in virtue of their flavoring qualities [44].

Since the conquest, and notably in the last 60 years, the native diet has suffered great changes, due to the substitution or elimination of the milpa agro-ecosystem. In the Municipality of Zapotitlan, and all the regions, the system has been replaced in vast lengths by grasslands of African gramineae, cane fields, and commercial agave plantations, and in other extends areas the milpa has turned into maize monocultures, via government programs [48]. The changes in the native diet have been augmented by the implementation of NGO and government assistance programs intended to promote the consumption and production of meat, milk, and eggs, as well as the consumption of industrial food rich in sugars, wheat flour, and trans fats. The high intake of these products and the changes in the native diet could, not entirely, explain the accelerated increment in the rates of decalcification, cholesterol, diabetes, and obesity [52]; the general health deterioration of the native population could partially be due to this shift away from a diet based on vegetable products with high contents of fiber, calcium, potassium, probiotics, and low contents of sucrose, animal fats, and lactose, a diet that is the result of biological and cultural adaptation spanning 10,000 years [53–56].

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Chapter 5
Biodiversity and Edible Plants of Mexico

Cristina Mapes and Francisco Basurto

Abstract Mexico that stands out as a megadiverse country is the fifth nation in terms of species richness. The country is home to 25,000–30,000 species of plants and currently 7461 useful plants are registered, of which 2168 are edible according to ethnobotanical data base of Mexican useful plants (BADEPLAM). In this chapter, edible plants are divided into six subcategories and describe some of the edible species recorded across different ethnobotanical research conducted in different regions of Mexico. We conclude that although the food habits in the country have undergone drastic changes in recent decades, and not always for the better, numerous food plant resources in Mexico continue to be widely utilized mainly by rural populations.

Keywords Edible plants • Mexico • Nutrition • Ethnobotany • Biodiversity

Biodiversity in Mexico

Almost two-thirds of the world's biodiversity concentrates in a little over a dozen countries known as megadiverse countries. Mexico is noticeable as a megadiverse country because it occupies the fourth place in species richness, and because it combines this high biodiversity with a high cultural richness [1].

Almost all of the climatic groups are represented in the territory of Mexico in an area of only 1.3 % of the world's total. This accentuated climatic variation is due to a number of factors, among which are: the country's location between the neartic and the neotropic, on the border separating the dry and humid climates (marked by the Tropic of Cancer), the tapering of its width towards the southern border—only a fraction of the length of its northern border, and the extension of its coastline rising the humidity in the southern part of the country [2].

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The roughed relief of Mexico contributes further to its climatic heterogeneity. The altitudinal range from the coastal areas to the higher elevations of the Oriental and Occidental Sierra Madre goes from a few meters to over 2000 meter above sea level (m.a.s.l.). The elevation reaches to 5000 m.a.s.l. at the peaks of some volcanic mountains such as the Pico de Orizaba, Popocatépetl, and Iztaccíhuatl. Thus, the Mexican topography is one of the most uneven in a planet with an average elevation of 800 m.a.s.l. [3]. In the nearly two million square kilometer territory of Mexico, coastal plains give way to high elevation in mountain ranges, and to extensive plains in the central and southern portions of the country [2, 4, 5].

The climate and physiography of the Mexican landscapes originate multiple coexistent environmental conditions, thus generating a large variety of habitats occupied by thousands of different organisms [6].

But the history of the flora and fauna of the territory is also extremely important for explaining the splendor of Mexican biodiversity. Tropical species dominate in Central South America due to its closeness to the equator, while a flora and fauna of Boreal origins populates North America with its colder climates and well-marked seasons. Mexico is placed in the intermediate zone between the southern and northern extremes of the American continent because of which it harbors a combination of tropical and temperate species. Boreal affinity species occupying mountainous areas with colder climates, and tropical species located in lower elevation areas with dry or humid climate, confort a diverse mixture of species exhibiting high richness and uniqueness in all possible aspects [7, 8].

Mexico occupies the second place in the world in number of species of reptiles [9]. As to mammals, 535 species live in Mexico of which 488 are terrestrial and 47, marine [10], a number only surpassed by Indonesia (667 species of mammals), and Brazil (578 species).

Besides this impressive number of species, the country is characterized by having a high number of species that are exclusively distributed within its national borders, i.e., found nowhere else in the planet. These species are known as endemic. Mexico is the country with the highest number of endemic species of terrestrial mammals, and between 20 and 30 % of its plant species are also endemic [7]. Over half of the species recorded in Mexico for some groups—such as pines, agaves, nolinas, araneids, and amphibians—are unique to the country [11].

Mexico is one of the five countries in the planet having the largest number of vascular plant species to date little over 25,000 of these having been described from a total estimated to be between 27,000 and 30,000 [1]. The flora of Mexico, containing 48 % of the planet's total number of species of the genus *Pinus*, 42 % of species in the family Cactaceae, and 75 % of those in Agavaceae. In terms of animals, the situation is similar: 32 % of the world's species of marine mammals, and 10 % of those of birds and reptiles live in Mexican landscapes [2].

Rzedowski [12] developed the most commonly used classification of the vegetation of Mexico, identifying the main plant associations according to physiographic, climatic, edaphic, and physiognomic characteristics. Ten general vegetation types are recognized in this classification, including forests, scrublands, grasslands, and wetland vegetation. According to the estimated original extension of each one of these vegetation types, most of the territory of Mexico was covered with xerophylous scrubland (38 %), followed by conifers and oak forests (19 %), and tropical deciduous forests (14 %) [2]. These extensions have, however, been altered by numerous and varied processes of modification of the original land cover, such as urbanization, agriculture, cattle rising, forestry, and repeated fires [11].

While species number is only one of the attributes of biodiversity, it remains to be one of the best indicators of biological richness.

Just as biodiversity is unevenly distributed throughout the planet, variations are also found within the country. In general terms, the humid areas of southern Mexico register the highest levels of plant species richness, while the largest centers of endemism occur in the arid northern zones [7]. The states of Oaxaca, Chiapas, Veracruz, and Guerrero have the bulkiest floristic lists in the country, each one with between 8000 and 9000 species. This distribution is explained by the presence in the Lacandon (Chiapas), Chimalapas-Uxpanapa (Oaxaca), and Los Tuxtlas, (Veracruz) regions of important areas of perennial rainforests, the world's most diverse ecosystem, and of deciduous forests in the case of Guerrero (Balsas River Basin) [7, 8].

Mexico is a diverse country not only biologically, but cultural too. The rich cultural mosaic of Mexico expresses in the numerous indigenous languages spoken in its territory, which depending on the classification criteria applied range from 59 to 291 in 68 groups within 11 linguistic families. Assuming 291 languages, the country includes 30.2 % of the continent, and 4.2 % from the world's totals. However, 364 linguistic variants have been recognized that should properly be considered as languages, thus Mexico is within the top ten countries in the world with the highest linguistic—and hence cultural—richness [1].

The past and existing cultures in Mexico have developed a close relation with the biodiversity present in their surroundings; both in terms of cosmovision and in the ways they have appropriated the available natural resources [1].

The country is one of the main centers of plant domestication [13, 14] and one of the main points of plant selection and domestication, where both processes remain valid and active.

Mexico has given the world over 118 species of domesticated plants useful as food, textiles, colorants, ornaments, and other uses [4]. Over 15 % of the plants consumed as food in the planet were originated in Mexico.[1].

According to the Ethnobotanical Database of Mexican Plants (BADEPLAM), 7461 useful plants have been recorded in Mexico until the present, of which 2168 are edible.

The Edible Plants: Wild, Domesticated, and More

The edible plants of Mexico could be cultivated, wild, crop weeds, or ruderal. According to De Wet and Harlan [15], the main difference between wild, crop weed, and domesticated plants is their increasing degree of dependence on humans for survival; this being maximal in domesticated and null in wild plants. Crop weeds and ruderal plants are independent from humans for their survival; despite they grow in a habitat created by people (disturbed land).

There is an ample spectrum known of modalities of human management of wild, crop weed, and ruderal plants. Many of these plants can be considered to be wild, but others are favored, protected, semi-cultivated, or even actually cultivated by people. In some cases, it can be said that these plants are undergoing a processes of incipient domestication.

According to Casas et al. [16], several forms of management status exist:

1. Gathered plants. This category includes plants from primary and secondary vegetation that are directly extracted from nature by people.
2. Tolerated and favored plants. Some wild plants are tolerated during clearing for house building or for cropping. Herbaceous crop weeds also belong in this group, some of which are tolerated because they are used for food (mostly as *quelite*), people only eliminating those plants that compete with crops or are useless.
3. Favored plants. This group includes cases of management intended for enhancing dispersion or growth of some plants in order to increase their availability. Some crop weeds have a particular interest for cultivators, so they not only are tolerated but also promoted by dispersion in crop fields of their propagation structures.
4. Cultivated plants. Occurs when in conscious way propagules of the plant of interest are distributed in plots specifically prepared for that purpose (plowed and weed-free). Some crop weeds are also cultivated in some regions of Mexico, such as the *alaches* (*Anoda cristata*), *chipiles* (*Crotalaria* spp.) and *papalo* (*Porophyllum macrocephalum*), both in association with other plants in milpas or chilares (chili fields) or as monoculture.

Some species may be subjected to more than one type of management. Farmers can gather, tolerate and protect, favor, or cultivate a particular species of crop weed, even in the same field.

Plants and Feeding

According to the book *Plato del Buen Comer* [17], foodstuffs can be distributed in three groups:

(a) Fruits and Vegetables. Sources of vitamins, minerals, water, and fiber.
(b) Grains and cereals. Provide energy, and if consumed whole, also fiber.
(c) Legumes and animal foodstuffs. Rich in protein and in energy from oils and fats in oleaginous seeds and meat. Legumes are also a source of fiber.

As can be seen in the eatwell plate, plants have a fundamental role in an adequate, nutritious, and balanced diet. In addition, many plants contain the so-called functional or nutraceutical elements, i.e., substances that besides forming a part of the diet can also prevent given ailments.

Edible plants are divided into seven subcategories:

1. Cereals, grains, and seeds.
2. Fruits
3. Vegetables
4. Roots and tubers.
5. Greens and *quelites*.
6. Drinks
7. Flowers

Some examples of edible plants are presented below.

Cereals, Grains, and Seeds

This group includes present and past food items of Mexican people: maize, beans, and squashes as well as species that were much more important in the diet during Prehispanic time, their present use having largely decreased. The dietary contribution of this group is mostly in the form of energy (carbohydrates and lipids) and protein, representing the basic diet in terms of amounts ingested. In the case of maize and beans in rural zones, the average daily per capita consumption is estimated to be of about 300 and 70 g, respectively.

The species mentioned in the following paragraphs can mostly be considered as accessory or emergency foodstuffs because they are consumed eventually or in times of scarceness, or used in periods when maize is lacking, both in the past as in the present. However, these species continue to be used by several human populations, some of them also having a large potential as functional foodstuffs.

Corn. *Zea mays* L. ssp. Mays. Poaceae

Maize occupies a prominent place among Mexican edible plants, being part of daily meals as a basic foodstuff, and it is the country's most important crop from the alimentary, economic, political, and social perspectives.

Maize (*Zea mays* ssp. *mays*), one of the three crops feeding humanity, originated in Mexico through a process of domestication carried out by Mesoamerican people from the *teocintles* (*Zea* spp.) naturally growing in Mexico and parts of Central America (Fig. 5.1). The populations of teocintle from central Mexico or the Balsas River Basin are considered to be the ancestor plants from which maize was domesticated [18, 19].

The domestication process of maize began in Mesoamerica nearly 10,000 years ago and continues in the present by means of management, cultivation, and selection practiced year after year by maize farmers, as well as through the interaction of maize with their wild relatives, the teocintles, in regions where both naturally coincide.

Fig. 5.1 Capsules fruit “grains” scattered teosinte. Photo: Carmen Loyola

Fig. 5.2 Corn cobs. *Zea mays* L. Photo: Carmen Loyola

Mexico is the center of origin of maize and is probably the world’s area where the highest diversity of the plant exists and is the place where teocintles and other related grasses such as the genus *Tripsacum* evolved and grow. At present, 64 races of maize are recognized in Mexico, which are cultivated at elevations ranging from sea level to 3400 m.a.s.l. [20].

The ample diversity of maize in Mexico (Fig. 5.2) is used for preparing a large variety of foodstuffs including tortillas, tlayudas, tostadas, totopos, tamales (of various shapes, styles, and fills), atoles (simple, sour, sweet), gorditas, tlayoyos, pintos, pozol, tejate, tascalate, pinole, burritos (roasted maize kernels covered with

Fig. 5.3 Beans. *Phaseolus vulgaris* L. Photo: Cristina Mapes

unrefined brown sugar called piloncillo), palomitas (popcorn), tesgüino, esquiate, elotes (corn in the cobb), esquites, quesadillas, nicuatole, coricos, and others.

The development of preparation techniques of maize including nixtamalization, which is perhaps the most important [21], roasting, cooking either wet or dry, and fermenting, is as relevant as its domestication.

Maize is also the central element of the Mesoamerican food production agricultural system, the milpa. In the milpa system maize is planted in a particular order along rows, being a unique system of cereal cultivation. This structure allows for the association of maize with other crops, which can be cared for in an individualized way, and for cropping the products of the milpa (maize, bean, and squash and quelites) along different time periods and stages of development, i.e., elotes (corn on the cobb), ejotes (immature bean pods), squash fruits, and squash flowers.

Beans. *Phaseolus spp.* Leguminosae

Beans of *Phaseolus* spp. (Fig. 5.3) are one of the basic foodstuffs in Mexico, a country considered to be a diversification center and, most surely, the center of origin of the genus, because 90 % of its species are present in its territory.

Five domesticated species of beans are known to be cultivated in Mexico: *P. acutifolius*, *frijol tépari* or *escumite*; *P. coccineus*, *frijol ayocote*, *patol* or *tecomare*; *P. dumosus* (=*P. polyanthus*), *exoyema*, *acalete*, *frijol gordo*; *P. lunatus*, *frijol navajita*; and *P. vulgaris*, the common bean (*frijol*) with numerous names such as *negro*, *canario*, *flor de mayo*, *flor de junio*, *rosita*, *bayo*, *peruano*, *azufrado*, *alubia*, *ojo de cabra*, *mantequilla*, *americano*, *de milpa*, *enredador*, *garrapato*, and *sangre de toro*. Besides these cultivated forms, wild forms of four of the cultivated species are found in Mexico together with several forms intermediate between wild and cultivated.

Since long before the Spanish conquest, the production, storage, and consumption of beans were an essential and relevant part of agricultural culture in Mexico. After the conquest, with the introduction of new food plants and consumption habits beans and other native cultigens were displaced both from consumption and from production, nowadays being considered as low social status foodstuffs [22]. However, beans are an excellent source of protein and, together with maize constitute a balanced diet. Beans are rich in thiamine, riboflavin, niacin, and vitamin C, and can supply the human daily dietary requirements of potassium, calcium, phosphorous, and zinc [23–25].

The extended time period of coexistence of Mesoamerican people with beans has resulted in a diversity of forms of preparation for its consumption, being eaten boiled with salt, or supplemented with green chili pepper and edible greens (*quelites*) such as *xocoyoli* (*Begonia* spp.), tequelite (*Peperomia peltilimba*), or leaves of *gásparo* (*Erythrina americana*). Beans can also be eaten fried or inside *tamales* and maize *gorditas*, either ground or as tender grains and sometimes spiced with avocado leaves. Some varieties of the common bean can also be prepared roasted and ground, the resulting meal being boiled in water as a sort of gruel. The tender leaves, flowers, root, and tender legumes of bean species are also eaten.

Squash Seeds. *Cucurbita spp.* Cucurbitaceae

Squashes (*Cucurbita* spp.) are the first plants to appear in the archaeological records of caves in Ocampo, Tamaulipas and Tehuacán, Puebla, and are considered to be among the first domesticated plants [26].

Mexico is considered to be a center of diversity for the genus *Cucurbita*, and four of its five domesticated species are Mesoamerican: *Cucurbita argyrosperma, C. ficifolia, C. moschata*, and *C. pepo* [27, 28].

Squashes (Fig. 5.4) have an integral use as food plants, i.e., all of its parts except for the roots are used for food. The tender leaves, stems and tendrils, flowers, immature and mature fruits, and seeds are used as food.

From a nutritional standpoint, seeds are rich in protein and oils, and although seeds of four domesticated species are consumed, two are the most relevant as sources of edible seeds: *C. argyrosperma* and *C. pepo*.

Seeds are eaten roasted as snacks and are also prepared in *moles* and *pipianes*. Squashes, together with maize, beans, chili peppers, and numerous *quelites* form the base of the agricultural production system called *milpa*, which is considered to be the basic food production system that gave origin to, and sustained Mesoamerican cultures [27].

At present, squashes used for seed production are cultivated in monoculture, but the cultivation of squashes in the milpa continues to be highly important for indigenous and mestizo rural populations in several regions of Mexico. The importance of squashes in the *Todos Santos* festivities, perhaps one of the most important and diffused in Mexico, must be underlined.

Fig. 5.4 Squash. *Cucurbita* moschata L. Photo: Francisco Basurto

Piñones. *Pinus* spp. Pinaceae

The highest diversity of piñon pine species is located in Mexico, with 13 species: *Pinus catarinae, P. cembroides, P. culmicola, P. discolor, P. edulis, P. johannis, P. juarezensis, P. maximimartinezii, P. monophylla, P. nelsonii, P. pinceana, P. quadrifolia*, and *P. remota* [29–31].

The piñón pine species are distributed mostly in northern Mexico in the states of Aguascalientes, Baja California, Baja California Sur, Coahuila, Chihuahua, Durango, Guanajuato, Hidalgo, Jalisco, Nuevo León, Puebla, Querétaro, San Luis Potosí, Sonora, Tamaulipas, Tlaxcala, Veracruz, and Zacatecas. In general, piñon pines are low trees, mostly less than 10 m in height, growing in low precipitation zones receiving 300–600 (1000) mm of annual rainfall [30, 32].

Pinus cembroides is the more amply distributed piñon pine and that with most commercial importance, followed in productive importance by *P. nelsonii* [31]. Most Mexican piñón pine species are endemic, some having very narrow distribution areas, such as *P. maximartinezii* from southern Zacatecas, and *P. culminicola* from southeast Coahuila and central western Nuevo León [29, 30]. Pinions are mostly used in Mexico in desserts or as a snack.

As food, pine nuts are rich in protein and lipids. The production in Mexico of piñon is derived from gathering of wild populations. Nuevo León is the leading state in production of piñon, but the nuts are also commercialized in the states of Hidalgo, Tlaxcala, and Puebla [33, 34].

Chia and Chan. *Salvia hispanica* L. and *Hyptis suaveolens* (L.) Poit Lamiaceae

Most chroniclers mention the importance of chia in pre-Columbian Mexican beverages and food. Reports of culinary uses of chia seed (*Salvia hispanica* L.) (Lamiaceae) include the use of whole seeds, seed flour, seed mucilage, and seed oil. A common practice of roasting and grinding of the seeds into flour—known as *chianpinolli* mimicked the processing of *pinole* maize, and often both seeds were processed together. The *chianpinolli* became incorporated into tortillas, tamales, and various aztec beverages known as *chianatole* (from Nahuatl, *chianatolli*).

Since 1600, the refreshing drink made with whole chia seeds has attained great popularity in Mexico, peaking in the eighteenth and nineteenth centuries with corner vendors and innkeepers selling the product throughout Mexico. Many Mexican households still favor the beverage calling it *agua de chia* or *chia fresca* [35].

Between the years 1932 and 1935 in Mexico, an annual average of 74 ha were sowed in the states of Jalisco, Puebla, Michoacán, Guerrero, Oaxaca, and Chiapas. Currently, it is cultivated in Acatic, Jalisco, Atzitzihuacan, Puebla, and Olinalá, Guerrero [36].

Chia seeds also have other culinary uses including the preparation of flour, mucilage, and cooking oil. Chia oil is high in omega-3 linoleic acid and natural antioxidants. The mucilage from seed coats is a polysaccharide useful as soluble fiber, and the seed has high contents of protein and oil [36].

The *chan* (*Hyptis suaveolens*) was also extensively cultivated in pre-Columbian time for its edible seeds. In many parts of Central America, seeds of chan are used in beverages similarly to those made from chía (genus *Salvia*). The seed is highly important in .the state of Colima, Mexico, where vendors go door-to-door selling the ground seed.

Cachichín or Cacaté. *Oecopetalum mexicanum* Greenm. and C.H. Thomps. Icacinaceae

The tree is distributed in the Sierra de Misantla—located in central Veracruz, Mexico—and is locally known as *cachichín*. The tree is abundant in the transition between perennial tropical forest and cloud forest between 400 and 1100 m.a.s.l. The seeds are gathered in three traditional agroecosystems: shade coffee plantation, *cachichinales* in which the almost exclusive growth of cachichín is favored, and natural forests [37].

Gathering starts during April and finishes by mid May, although fruits can be found until early June. Fruits are picked when green, and sometimes when brown colored. Each day's crop is taken to houses and extended to dry them. Small boards separate the fruit in order to keep track of the different harvests. Cachichín is commonly consumed roasted, having a bitter flavor and a consistency similar to that of peanuts. The fruit's husk (exocarp) is removed with the teeth before consumption of seeds, given it is always sold husked. Its fruit is picked from the ground for its edible seeds, which are regionally marketed.

Consumption, management, and gathering of cachichín seeds are significant recreational activities. Cachichín seeds provide food and economic resources to numerous families in the Sierra de Misantla region [38].

In Chiapas, this specie is called cacaté and used as food for zoque, tzotzil, and mestizo people [39]

Piñón, Piñoncillo, Xuta. *Jathropha curcas* L. Euphorbiaceae

It is a plant native to Mexico commonly known as *piñón* that has gained notoriety due to its relevance for the production of biofuel. It is a 1–8 m tall draught-tolerant tree growing on poor and sandy soils in tropical and semitropical climates at elevations going from 5 to 1500 m.a.s.l. Its seeds have high protein (25–30 %) and fat (55–50 %) contents. It is well known in many rural communities in southeastern Mexico, where the inhabitants of the regions consume them after being roasted and in traditional dishes. The seeds are used as snack or in stews, tamales, and atoles [40].

It has been considered to be toxic due to the presence of phorbol ester alkaloids having purgative and other effects. Non-toxic varieties (*piñón manso*) have been found only in Mexico. The piñón manso is more frequently found in dooryard gardens, and the toxic piñón, in live fences [40].

Ramón, Breadnut, Maya nut. *Brosimum alicastrum* Sw. subsp. *alicastrum* C.C. Berg. Moraceae

Ramón is one of the dominant tree species growing in perennial and sub-deciduous tropical forests along both coasts of Mexico. Its scientific name is derived from the Greek *brosimus*, meaning edible.

The tree is popularly known as ramón, capomo, ojche or ojite, having also names in several of the country's native languages [41]. The name ramón is derived from the Spanish term *ramonear*, referring to the browsing by cattle and other domestic animals of its seeds and leaves, its seedlings also being grazed on [42].

Ramón are dioecious tall trees that fructify between March and June. The red fruit is about 2 cm in diameter and usually contains a single seed. The fresh pulp of the fruit and the seeds are edible, the latter being either consumed fresh or dry to be cooked, ground, and incorporated to maize dough to prepare tortillas. The leaves of the tree are a good fodder [43]. The roasted and ground seeds are used as a coffee substitute and for preparing a dark colored dough used for making bread or tortillas. Boiled in water, it is recommended for convalescing patients. Ramón trees are particularly abundant in Maya archaeological sites, this distribution suggesting their management and cultivation by this ethnic group for its use as food [43]. From a nutritional standpoint, ramón seeds are rich in carbohydrates and over 12 % of its dry weight is of crude protein with high content of tryptophan (an amino acid in which maize is deficient), and also contain calcium, phosphorous, iron, and vitamins A, B, and C [43].

Despite the potential of ramón as a human foodstuff, only in the state of Veracruz the estimated annual production of dry seed being of 80,000 t [42, 43], its current use is restricted only to some regions of the country, where it is seasonally consumed. Instead, ramón is reported as an emergency foodstuff used in times in which maize crops are scarce [44], a form of use that is becoming more rare due to the increased access of rural communities to maize due to the development of roads, besides that forest groves where ramón grows can be relatively distant from human settlements.

Chamal and Tepezintle. *Dioon edule* and *Ceratozamia mexicana*, Zamiaceae

The chamal and tepezintle are two species of the family Zamiaceae having edible seeds, both included in the Mexican Official Norm NOM-059-ECOL in the category of in risk of extinction due to their extraction as ornamental plants, and to a lesser extent, also due to the use of their leaves as a church ornament during the patronal and All Saints festivities.

The chamal, also known as tiotamal or quiotamal, is endemic to the Gulf of Mexico region with presence in the states of Veracruz, Puebla, Hidalgo, Querétaro, San Luis Potosí, Tamaulipas, and Nuevo León [45, 46], where it grows in ecotone zones between the deciduous tropical forest and the oak forest

Although recognized as a toxic plant for humans and cattle, in Querétaro and San Luis Potosí the seeds of this plant are used as food [45, 47]. Seeds of this species are gathered from wild populations and prepared in tamales, tortillas, atoles, and gorditas after being cooked with ashes and lime. Chamal use as food is restricted to the Xi'ui people as an emergency foodstuff for times of scarcity, but chamal tamales are also prepared to be sold in the Huasteca Potosina [47].

The tepezintle (*Ceratozomia mexicana*) grows associated with the mountain cloud forest and is distributed in San Luis Potosí, Hidalgo, Querétaro, Puebla, Veracruz, Tamaulipas, Chiapas, and Oaxaca [46]. It is extracted from wild populations and in the Sierra Norte de Puebla its seeds are consumed roasted as a snack, or boiled to be added to maize dough for making tortillas [48].

Guaje, Huaxi, Nduva, Iya. *Leucaena spp*. Leguminosae

The immature and mature seeds of species of guaje are consumed, and the flower buds, immature foliage, and insect gals of some species are also eaten. The more important species reported to have edible seeds are *L. esculenta* and *L. leucocephala*, other similarly consumed species being *L. macrophylla*, *L. lanceolata*, *L. collinsii*, *L. cuspitata*, *L. confertifolia*, *L. diversifolia*, and *L. pulverulenta*, the use being reported from the states of Oaxaca, Puebla, Guerrero, Morelos, Veracruz, Hidalgo, San Luis Potosí, Querétaro, Chiapas, Chihuahua, and Michoacán [49]. The species of the genus are under different intensities of human management going

Table 5.1 Proximal analysis of guaje seeds (% dry weigth)

Moisture	82.00
Ash	5.64
Ether extract	2.79
Crude protein	27.81
Fiber	29.00
N free extract	34.76
Kcal/g	275

from wild, protected, favored, and cultivated [49, 50], and it is frequent to see them sold in numerous weekly markets (tianguis), with a tradition of consumption dating to Prehispanic times.

In general, the immature, green seeds are eaten raw to accompany meals, but mature seeds are also eaten after being roasted. Grounded roasted seeds are made into cakes that are sent to migrant workers in the USA. In the Mixteca region, guajes are prepared in a typical dish called guaxmole (from Nahuatl *uaxin*, guaje, and *molli*, stew, meaning guaje stew). Guaxmole is a chili and meat soup flavored and scented with the addition of guaje seeds. As many legume seeds, guajes are rich in protein (Table 5.1).

Fruits

Edible fruits are excellent sources of vitamins and minerals, but are also rich in sugars and other carbohydrates. Native fruits are found in all climatic zones of Mexico, where the inventory is estimated to be of over 200 species [51].

Mexico is an important producer of fruits at the global scale; however, some of the cultivated species not being native to the country such as the citrus fruits (oranges, limes, and lemons), mango (*Mangifera indica*), and bananas (*Musa acuminata* Colla×*M. balbisiana* Colla). Some relevant fruit species that are native to Mexico are the papaya (*Carica papaya*) and the avocado (*Persea americana*).

Fruits from arid zones are the tunas and xoconostles (fruits of the prickly pear plant, *Opuntia*), and the pitayas (fruits of *Stenocereus*), pitahayas (fruits of *Hylocereus*), and other cactus family fruits such as the chiotilla (*Escontria chiotilla*) and garambullo (*Myrtilocactus*). In humid tropical areas, people consume several classes of zapote (see below) and papaya. The capulín (mountain black cherry, *Prunus serotina*) and tejocote (Mexican hawthorn, *Crataegus mexicana*) are characteristic of temperate zones.

This category includes species with fruits having a characteristic sweet and sower flavor due to their pulps being chemically composed of a mixture of sugars and organic acids, mainly tannic, that besides a better nutritional content, confer agreeable and varied flavors to the traditional diet based on maize, beans, and chili.

Tunas and Xoconostles, Prickly pears. *Opuntia* spp. and *Cylindropuntia imbricata* Cactaceae

The tunas and xoconostles are fruits of genus *Opuntia*, plants of cactus family, which originated in the American continent, Mexico being considered as a center of its biodiversity. There are 86 species of *Opuntia*, of which 80 are native to the country.

Tunas differ from xoconostles in the former being sweet, while the latter are sour. Tunas are eaten fresh and xoconostles are generally consumed cooked.

The species of the genus *Opuntia*, called nopales, a term derived from the Nahuatl *nopalli*, are shrubby cactuses with flattened branches with a few or many spines having colorful flowers. The Nahuatl term *nochtli* designates the edible fruits of the nopales and *xoconochtli* mean *nochtli* sour.

The term *tuna* was introduced by the Spanish conquerors from the Caribbean and refers to the fruits of the nopales which are among the main fruits produced by cactuses worldwide.

This group of plants has a high importance in arid and semiarid zones, where many species are found.

The use of *Opuntia* spp. as food was recorded in the archaeological records of the caves Ocampo, Tamaulipas, and in Tehuacán, Puebla [52]. Ten tuna producing species of *Opuntia* are known, the most important being *O. ficus-indica*, *O. streptacanthae*, and *O. lindheimeri*, which can be either cultivated or the fruits gathered from wild populations [53, 54]. Tunas are produced on a surface of nearly 70,000 ha in the semiarid regions of Mexico in the states of Zacatecas, San Luis Potosí, Aguascalientes, Guanajuato, Mexico, Nuevo León, Hidalgo, Guerrero, and Tlaxcala, and in the Baja California Peninsula [54, 55].

The xoconostles producing species are *O. joconostle* (xoconostle), *O. matudae* (xoconoxstle), *O. heliabravoana* (xoconstle blanco), *O. leucotrica* (coyonostle), and *Cylindropuntia imbricata* (xoconostle), grown in three main regions: central northern Mexico (Zacatecas, San Luis Potosí, Aguascalientes, Guanajuato, Querétaro, and Jalisco), central southern Mexico (State of Mexico, Tlaxcala, Hidalgo, and Puebla). Small plantations are established in northern Mexico (Baja California, Baja California Sur, Durango, Coahuila, Nuevo León, Tamaulipas), and in Michoacán, Morelos, Oaxaca, and Veracruz [55].

As mentioned above, xoconostles are generally eaten in stews, as desserts, and in marmalades, and tunas are mostly eaten fresh, but since Prehispanic times they are also used for elaborating several preparations and beverages, such as a fermented beverage of tuna juice called colonche prepared in the Potosino Zacatecano, candied tunas, sun dried tunas, and in preparations made by crushing and cooking the tunas: miel de tuna (tuna honey), melcocha, and queso de tuna (tuna cheese) [56].

Pitayas and Pitahayas, Dragon Fruit. *Stenocereus* spp. and *Hylocereus* spp., *Selenicereus megalanthus* (K. Schum. ex Vaupel) Moran. Cactaceae

Besides *Opuntia*, the main edible fruit producing cactuses throughout the world are the pitayas (*Stenocereus* spp.) and the pitahayas (*Hylocereus* spp., the dragon fruit, and *Selenicereus megalanthus*).

Fig. 5.5 Pitahaya. *Hylocereus undatus* (Haw.) Britt & Rose. Photo: Francisco Basurto

The main producer countries of pitahayas are Nicaragua, Colombia, Mexico, Guatemala, and at present, Israel is increasing in importance both in breeding and in management of the crop, becoming a strong competitor in the market of the fruit.

The fruits of pitahayas are ovoid, measuring up to 12 cm in length. The rind is pink colored and has scales. The pulp is generally white, soft, has a pleasant semi-sweet flavor, and has numerous, very small seeds. The fruits mature between June and August (Fig. 5.5).

In Mexico, pitahayas have an ample variety of uses and about 20 species of *Stenocereus* are known as pitahayas, most of them native to the country. The more extended use is consumption of the fresh fruits, in beverages, sherbets and ice creams, and in marmalades. Pitahayas are collected from wild populations, cultivated in dooryard gardens, and recently, in plantations. Cultivation of pitahayas has an advantage over other crops due to its low water requirements. The cactus is able to survive in steep hillsides and requires little management, although it has been demonstrated that their productivity increases significantly with irrigation, fertilization, pruning, and soil management and conservation practices [57].

Jobo y Ciruelas, Abales o Jocotes. *Spondias mombin* L. y *S. purpurea* L. Anacardiaceae

The fruits of two species of *Spondias* are highly valued in Mexico: *S. mombin* and *S. purpurea*. Both are distributed from Mexico to Panama [58], in Mexico being present in both coastal slopes from Sonora to Chiapas, and from Tamaulipas to Yucatán and Quintana Roo.

The jobo, *S. mombin*, grows in higher humidity areas in perennial and sub-deciduous tropical forests, while the jocote, *S. purpurea*, is from deciduous tropical forests, both species being components of the dominant strata [41]. The jocote is more amply distributed, has a higher economic importance, and is more used than the jobo.

Jobo fruits are consumed fresh, in refreshing beverages, marmalades, and liquors. The trees of jobo are grown in dooryard gardens, diversified coffee plantations, and in living fences, bot is not grown as a monoculture. It is mostly used for self-consumption and is sold during the harvest period in local and regional markets.

The jocote has two centers of domestication, one from southern Mexico to Panama, and another one in central western Mexico [58].

Fruits of *S. purpurea* have a long tradition of consumption in Mexico since Prehispanic times [59] and its consumption persisted during the Colonial period [60].

In Prehispanic times, jocote fruits were gathered from wild populations, forming part of the diet of native peoples from the tropical regions of Veracruz. Intensive cultivation of *S. purpurea* in western Mexico began in the nineteenth century, peaking in the end of that century and the beginning of the twentieth century [61]. In present times, the fruits of jocote are gathered from cultivated and wild populations in several tropical and subtropical regions of Mexico [62]. The fresh fruits are eaten mature or immature, pickled in alcohol or brine. The fruits are used for preparing refreshing beverages and vinegar; they are also used for preparing gelatin and jelly. Immature fruits are added to beans, and atole, pies, and sauces are made from them. Young sprouts and leaves are consumed raw or cooked as vegetables. The fruits are used for self-consumption and are amply sold in local and regional markets. The fruits of jocote have an ample diversity of color and shape, being purple, red, orange, yellow, or green colored, and their shape can be elongate or semispherical, and either small or large.

Guamuchil, Huamuchil or Pinzán. *Pithecellobium dulce* (Roxb.) Benth. Leguminosae

The guamúchil forms part of the deciduous tropical forests [41], being distributed along the Pacific slope of Mexico from Sonora and Baja California Sur to Chiapas, and also in the Huasteca region (Tamaulipas, San Luis Potosí, Hidalgo, and Querétaro) and the Yucatan Peninsula.

The flattened, black colored seeds of guamúchil are surrounded by a white or reddish colored fleshy aril that is edible and of a sweet flavor. It is used as a sweet and for preparing refreshing beverages. It is mostly consumed fresh as a sweet [63].

Fresh fruits consumed in large quantities can *close* the throat due to their high content in tannins, but despite that, are appreciated by people in rural communities that eat them directly or seasoned with salt, powdered chili, and lime juice.

In Xochitepec, Morelos the fruits of guamuchil exist in two flavors, one sweet and sour consumed fresh or in atole, the other bitter and called *atorón* or *ahogadizo*, Spanish words referring to their unpalatability, making them difficulty to be swallowed. This bitter guamuchil is prepared in sauces, which can be green or red according to preference. For their preparation, chili peppers are previously fried in a small amount of lard or oil and grounded together with fruits of guamuchil *atorón* (or the sweet variety), garlic, onion, and salt to taste [63].

Atole of guamuchil is prepared in a pot with maize dough diluted in water and, while this boils, sweet flavor guamuchil fruits are ground and mixed in, finally sweetening the preparation with molasses water or refined sugar.

The commonest way of consumption is fresh, as a snack eaten by peasants during their brakes along their long workday in order to hold on until the next meal [63].

In other regions of Mexico the fleshy, sweet flavored white or reddish aril that surrounds the black colored seeds is eaten as a sweet and for making a refreshing beverage. In Sinaloa, syrup is made with the aril, water, molasses, and cinnamon; atole is also prepared from the aril. The Yaqui people make tortillas from maize dough to which guamuchil is added [64].

Nanche, Changunga, Golden Spoon. *Byrsonima crassifolia* Kunth. Malpighiaceae

The nanche is amply distributed in tropical and subtropical Mexico. Pennington and Sarukhán [41] mention nanche as a component of savanna vegetation in codominance with *Curatella mexicana* (raspa viejo) and *Crescentia cujete* (cuatecomate, tree gourd).

Nanche fruits are of high nutritional value. Analyses show it contains high amounts of vitamin C, sometimes rising up to 369 mg/100 g, and up to 650 mg/100 g of vitamin A, the latter concentration surpassing that in mango. Nanche fruits are consumed fresh for their exquisite scent and sweet and sour flavor, having high potential for its industrialization, either in bottled drinks, sweet concentrated pulps (ates), marmalades, sherbets and ice creams, liquors, etc. [65].

Siricote or Cupapé. *Cordia dodecandra* DC. Boraginaceae

Siricote is a dominant tree species in deciduous tropical forests growing in the Yucatan Peninsula. It is naturally distributed from southwest Mexico to Guatemala, Belize, Honduras, and in the island of Cuba.

Its fruits are edible and are eating in fresh or prepared in preserves [39].

Cuayote *Gonolobus* spp., Apocynaceae

The immature, green fruits of the species of the genus *Gonolobus* (Apocynaceae) are consumed roasted. In the Central Depression of Chiapas, the fruits are preserved in syrup and their seeds are eaten as popcorn after being boiled or roasted [66].

The species of *Gonolobus* in Yucatán are herbaceous vines growing in low and medium sub-deciduous tropical forests whose fruits are eaten roasted.

Among the Purépecha from Michoacán, women and children collect them from the wild, and afterwards roast in a fire made in the field and consume them; the gathering party joins in a lively congregation [67].

The Sapotes

The family Sapotacea, originating from Central America and Mexico, is among the fruit producing tree species. The name of the family and the words *zapote* and *sapote* are derived from the Nahuatl term *tzapotl*, a name applied to soft and sweet fruits having elongated seeds. Other families such as Chrysobalanaceae and Ebenaceae also have fruit trees known as zapotes.

Zapote Chico, Chicozapote, Sapodilla. *Manilkara zapota* (L.) Van Royen, Sapotaceae

The chicozapote (from Nahuatl, *xicotzapotl*, from *xicotl,* bumble bee and *tzapotl*) is one of the more useful plants growing in forests from Campeche. The tree grows naturally in tropical forests throughout Mexico and Central America, reaching south to Venezuela and Colombia. The fruits mature between January and April.

In some zones, chicozapotes are grown more or less extensively. At present, the main products of chicozapote are its latex, used for obtaining chewing gum (in Spanish, chicle, derived from the Nahuatl, tzictli), and the fruit that is consumed raw, in preserves, and in sherbets and ice cream. Despite that the exploitation of the latex has considerably diminished in southeastern Mexico, some centers of chicleros (people that extract chicle from the forests).

Zapote Amarillo (Yellow zapote), Canistel, Caca de niño. *Pouteria campechiana* (Kunth) Baehni. Sapotaceae

The fruit of trees of *Pouteria campechiana* is edible and matures between June and October. The trees are distributed along the Gulf of Mexico slope from San Luis Potosí, northern Puebla and Veracruz, to the Lacandon forests and Yucatán, and in the Pacific slope from Nayarit to Chiapas. The zapote amarillo forms part of the high perennial, sub-deciduous, and sub-deciduous tropical forests, and it generally grows in elevations close to the sea level [41]. The zapote amarillo is grown in dooryard gardens from tropical dry and humid zones.

Zapote Mamey, Mamey colorado, Mamey, Mamey sapote. *Pouteria sapota* (Jacq) H.B. Moore et Stearn. Sapotaceae

Mamey trees originated in the humid tropical regions of the American continent and its natural distribution is not well defined because of its cultivation since Prehispanic times. It is probably native from southern Veracruz, Tabasco, and northern Chiapas.

It has been recorded to grow as part of tall perennial tropical forests of *Terminalia amazonia* in northern Chiapas.

The main use given to this species, and for which it has been extensively grown, is for consumption of its delicious fruit. Mamey exhibits a highly variable quality and has recently been object of selection to improve it [41]. The fruits are generally consumed raw, but are also used in sherbets and ice creams and in refreshing beverages.

Cultivation of mamey is associated with other fruit crops, including citrus fruits, ornamental and timber producing species. In Tabasco, mamey trees are used for shading cocoa, and in other regions of Puebla and Veracruz States for shading coffee plantations.

Caimito, Cayumito, Star Apple, Milk Fruit. *Chrysophyllum cainito* L., Sapotaceae

The caimito is a common tree in southeastern Mexico, particularly in the Yucatan Peninsula, where it is a part of orchards and dooryard gardens. The botanical name of this species refers to the golden color of its leaves. The tree originated in Central America and the Antilles and was introduced into Mexico.

Two varieties of caimito are known: one with dark purple colored fruits, and another one with yellowish green colored fruits. Both variants of the fruit have an edible, purple colored, fleshy and juicy pulp with traces of latex. In several regions, the fruits are appreciated as a supplementary foodstuff.

Zapote cabello, Zapote borracho, Tzontzapot, Sun sapote. *Licania platypus* (Hemsl) Fritsch. Chrysobalanaceae

The fruit of *Licania platypus* is eaten in some regions, where it grows wild or semi-cultivated. Despite being fibrous, the fruits of this tree have a pleasant flavor. It is distributed in the Gulf of Mexico slopes from Veracruz and northeastern Puebla to northern Chiapas, the Lacandon forest and the Chimalapas region, and in the Pacific slopes in Jalisco, Michoacán, and Guerrero. Although not being abundant, it is one of the tallest trees in tall and medium perennial and sub-perennial tropical forests growing at elevations between 300 and 600 m.a.s.l. [41].

Zapote Negro, Black Sapote. *Diospyros digyna* Jacq. Ebenaceae

The zapote negro is native to Mesoamerica, especially in Mexico and Guatemala. In Mexico, this specie is distributed on the Golf coast from northern Puebla and Veracruz to northern Chiapas and south of the Yucatan Peninsula; on the Pacific coast from Jalisco to Chiapas. Grown in perennial tropical forest, from sea level to 1200 m.a.s.l. [41].

The fruits of *Diospyros digyna* are commonly seen in markets. The pulp has a very agreeable flavor and is frequently eaten mixed with orange juice. The fruits are rich in calcium and ascorbic acid. The tree grows well in deep, clayey, and humid soils and is easily propagated by seed. It is cultivated in many tropical and subtropical zones away from its natural area of distribution. Its name is derived from the Nahuatl *tilzapotl*, composed of *tliltic*, black, and *tzapotl* [68].

Coyules y coquitos. *Acrocomia mexicana* Karw. ex. Mart. and *Scheelea liebnammii* Becc. Arecaceae

Coyol is the common name of the palm *Acrocomia mexicana*, which is derived from the Nahuatl *cuauhcoyollo*, meaning jingle bell tree, composed of *cuahuitl*, tree, and *coyolli*, jingle bell. The name alludes to the abundant spherical fruits. The palm is up to 15 m tall, its upper trunk being covered by spines and frequently covered by the hanging dead fronds. It is found along the Gulf of Mexico slope in central and western San Luis Potosí, northern Puebla, Veracruz, and the eastern Yucatan Peninsula. Along the Pacific slope it is distributed in the coastal areas of Nayarit, Jalisco, Colima, and Oaxaca. It is part of secondary vegetation derived from medium perennial and sub-deciduous tropical forests, at elevations from sea level to 800 m.a.s.l. Its fruits are edible and are sold in markets.

In the Central Depression of Chiapas, the palm is exploited from wild populations to obtain “taberna” an alcoholic beverage. Each year the palms suitable for harvesting are selected, which are those between 4 and 6 years of age that have flowered and fructified at least once [69].

During the dry season (February to April), local people cut down the selected palms and remove its leaves. Afterwards, a mouth or canoe is formed at the height of the sprout, in which the carbohydrate-rich sap runs down. The sap is naturally fermented with the heat and an alcoholic beverage is thus obtained known as taberna. In such conditions, a stem can produce between 3 and 6 L of taberna per day during 1 month. Popular knowledge holds that the phase of the moon has to be considered for determining the proper timing of cutting in order to obtain good quality taberna.

Taberna is customarily drunk directly from the canoe with the aid of a reed, or after pouring it into glasses to which ice, water, and sugar can be added to make it render further [69].

The coquito is the fruit of *Scheelea liebmannii* (=*Attalea butyracea*), a palm called coco, corozo, or coyol real, having edible seeds that are rich in fatty acids. The palm reaches up to 30 m in height and is distributed along the Gulf of Mexico slopes from northern Puebla and Veracruz to Chiapas and Campeche as a part of deciduous tropical forests. In conditions of perturbation, the palm forms nearly pure stands. It is also favored by people, because of which it is found in grazing lands, dooryard gardens, and coffee plantations [41].

Guayaba, Guava *Psidium guajaba* L. Myrtaceae

Guayaba trees originated in tropical America, from where it was transported to Europe during the sixteenth century, and from there to India and other Asian countries. Despite its Mesoamerican origin, India is the main producer of guayaba fruits with over 1.5 million hectares of the crop, and an annual production of 1.7 million tons.

In Mexico, the region Calvillo-Cañones in the states of Aguascalientes and Zacatecas is the major guayaba producing area with 12,000 ha, followed by eastern Michoacán with 9000 ha of the crop [70].

Guayaba fruit is an excellent source of vitamin C, besides containing niacin, vitamins B1 and B2, as well as minerals such as calcium, magnesium, iron, and potassium.

Aguacate, Avocado. *Persea americana* L. Lauraceae

Mexico is one of the countries with an ample diversity of *Persea americana*, the avocado tree with at least 20 related species (Fig. 5.6). The concept of races has been used for describing the variation of avocado, three being recognized worldwide, all present in Mexico: Mexican, West Indian, and Guatemalan. Classified these races as botanical varieties: *P. americana* var. *drymifolia,* corresponding to the Mexican race; *P. americana* var. *americana*, the West Indian race; and *P. americana* var. *guatemalensis*, the Guatemalan race [71].

The diversity of avocado was known since Prehispanic times, the Florentine Codex describing three types corresponding to the above-mentioned races or variet-

Fig. 5.6 Avocado. *Persea americana* L. Photo: Francisco Basurto

ies [72], respectively: *aoacatl* or *ahuacatl*, in Nahuatl meaning avocado, and figuratively, testicle; *quilahuacatl*, meaning green avocado, and considered as the best to eat; and *tlacazolahuacatl*, translated from Nahuatl as gluttony avocado, described as being larger than the aoacatl [73]. Morphological studies show a closer relation between the West Indian and Guatemalan races.

Races of avocado are distributed according to elevation and the freezing free zones. In general, the Mexican race grows in the temperate zone above 2000 m.a.s.l., the Guatemalan race in the subtropical zone between 1000 and 2000 m.a.s.l., and the West Indian race in the tropical zone below 1000 m.a.s.l. However, hybrids between these races have intermediate adaptation. An example of that is the Hass cultivar, an advanced hybrid between the Guatemalan and Mexican races, estimated to have between 10 and 15 % of genes from the latter race, which confers it a better adaptation to more temperate zones. The Mexican race predominates in pine-oak forests, the Guatemalan race is found in mountain cloud forests, and the West Indian race in perennial tropical forests, although very few trees of this race have been found growing naturally in such forests. The quetzal inhabiting in the El Triunfo Biosphere Reserve in Chiapas is a dispersal agent of wild avocado.

Consumed avocado ranges from fruit collected in natural forests to processed products. Avocado has deep roots in the Mexican diet. Avocado fruits are rich in minerals and A, D, and E vitamins. Avocado oil contains phytosterol, which makes it ideal for elaborating skin lotions and creams, soaps, dog food, and cooking oil [71]. The Mexican race of avocado (*P. a.* var. *drymifolia*), characterized by small fruits with thin rinds, is the richest avocado race in oil content (30 %).

Local people consume the fruits of *criollo* (creole, land races) avocado trees in the states of Michoacán, Puebla, and Mexico, and their leaves are appreciated as a condiment. Avocado and chinini (*Persea shiedeana*) trees are used in Mexico as shade trees in coffee plantations, their fruits are eaten and their boles are used as timber.

Papaya. *Carica papaya* L. Caricacea

Papaya is a pantropical species that originated in the American continent, but its exact place of origin remains unknown, possibly being from southern Mexico, Costa Rica, and other countries in Central America, northwestern South America or southern Brazil. At present, papaya is cultivated in all the tropical regions of the American continent. In Mexico, it is distributed along the Gulf Coast of Mexico from Tamaulipas to the Yucatan Peninsula, and along the Pacific slope from Baja California to Chiapas. It grows in secondary vegetation of tall perennial tropical forests.

Vegetables

Some species of vegetables are native from Mexico and, besides being part of the culinary tradition of the country tomato and chili have also become part of international cuisines, and in the case of chili, have acquired global high economic

Fig. 5.7 Tomato. *Solanum lycopersicum* L. = *Lycopersicon esculentum* Mill. Photo: Carmen Loyola

importance both as foodstuffs as in the food industry. Chili peppers are the most amply cultivated condiment plant in the world.

Jitomate, Tomato *Solanum lycopersicum* L. (=*Lycopersicon esculentum* Mill.) Solanaceae

Mexico contains a large variety of tomato being a center and diversification of the crop. Tomato is used from wild, various degrees of domestication, and cultivated populations. Within cultivated tomatoes, there is a range of forms going from small sized native or criollo varieties, ojos de venado (deer eye), arriñonados (kidney shaped), acostillados (ribed), and square, bell pepper types to the free pollinated and hybrid commercial varieties of the guaje (elongated) and bola (spherical) types (Fig. 5.7).

Mexico continues to be a natural reservoir of an ample variety of wild and cultivated tomatoes, deeply rooted in the cultural preferences of the country. Tomato is one of the most important crops in Mexico and the world, given that besides it economic importance is also a source of vitamins, minerals, and antioxidants [74].

Used in Mexican cuisine before the arrival of the Spaniards, currently the tomato is part of other cuisines in the world. In Mexico, it is a substantial part of hot sauces, chilpozontes (chicken or beef meat soup with chipotle chile) and is used as an ingredient in some mole sauces.

Fig. 5.8 Habanero chili. *Capsicum chinense* Jacq. Photo: Cristina Mapes

Chile, Chili Pepper. *Capsicum* spp., Solanaceae

There are four cultivated species of the genus *Capsicum* (Solanaceae) in Mexico: *C. annuum* native of Mesoamerica, *C. pubescens*, *C. chinensis*, and maybe *C. frutescens*, with nearly 25 species of wild and semi-domestic species [75]. According to the extent of its cultivation and economic value of its production, the chile verde (green chili pepper) *C. annuum* is the more important cultivated species in the world, Mexico being the country with the largest diversity of the crop. The wide range of adaptability of *C. annum* is due to the characteristics of pungency, flavor, scent, etc. that are essential for the preparation of dishes in the Mexican and other culinary traditions, besides its diverse uses in religious, medicinal, industrial, and other uses (Fig. 5.8).

Mexico is the main global exporter of chile verde, and the sixth exporter of dry chili pepper, its main importers being the USA, Japan, Canada, the UK, and Germany.

Capsicum annum is an essential part of Mexican diet and has a large number of forms, colors, and pungency levels. The chili peppers of this species receive different names and have different uses when fresh or dry (Table 5.2).

The peppers are the main ingredient of some of the iconic dishes of Mexico, such as moles, of which there is a great diversity, and chiles en nogada.

In Mexico, *C. annuum var grabriusculum* is the wild form of chili pepper, harvested in much of the country, it is also cultivated in the Totonacapan.

Table 5.2 Names and use of chili *Capsicun annuum*

Name in fresh	use	Name in dry	use
poblano, miahuateco	chiles rellenos chiles en nogada	ancho y mulato	mole poblano
chilaca	slices with egg (rajas con huevo)	pasilla	mole
jalapeño, cuaresmeño	pickled chiles rellenos	chilpotle (smoke dried)	chili sauce
mirasol, guajon	chili sauce	puya, guajillo	dressing (adobos)

Table 5.3 Edible use of husk tomato species

Species	use
P. angulata L.	sauces
P. chenopodifolia Lam.	fruit
P. coztomatl Moc. et Sesse ex Dunal	edible
P. gracilis Miers	fruit, quelite (greens)
P. nicandrioides Schledl.	sauces
P. philadelphica Lam.	sauces
P. santi-josephii Dunal	quelite (greens)

Tomate, tomatillo or tomate de cáscara, Husk tomato. *Physalis philadelphica* Lam. Solanaceae

The genus *Physalis* has its center of origin and diversity in Mexico, where wild, tolerated, cultivated, and domesticated species coexist, several of which are gathered for human consumption [76] (Table 5.3).

Of the 90 species recognized for the genus *Physalis*, 70 are endemic to Mexico [76], of which *P. philadelphica* is the most cultivated and has the largest commercial importance, representing one of the main vegetables grown in the country (Fig. 5.9).

Its use is reported since Prehispanic times and is mainly used for preparation of sauces in combination with green chili pepper (*Capsicum annum* L.). It grows in nearly every state of Mexico in warm, temperate, humid, and dry climates [76].

Husk tomato plants display ample morphological variation in the size of the fruit, with some recently bred lines and numerous local traditional varieties, the latter tending to be smaller and preferred locally for sauces due to its better flavor. In northern Puebla, it is frequent to see husk tomato stringed together as necklaces and sold in weekly markets or *tianguis*.

Roots and Tubers

In Mexico, a group of roots, rhizomes, bulb, and tubers are generically known as camotes (from Nahuatl *camotl* or *camotli*), all being rich in carbohydrates [77] and other nutriments (Tables 5.4 and 5.5).

Fig. 5.9 Tomatillo. *Physalis phyladelphica* Lam. Photo: Carmen Loyola

Table 5.4 Proximal analysis of 'camotes' (% dry weigth)

Species	Moisture	CH	Protein	E E	Fiber	Ash
Ipomoea batatas Camote amarillo	67.5	28.31	1.37	0.78	1.04	1.0
Ipomoea batatas Camote blanco	68.9	27.79	0.94	0.72	1.75	0.9
Manihot esculenta Guacamote, yuca	62.0	32.5	1.0	0.20	1.50	1.0
Xanthosoma sp. Pisis, Barbarón	71.0	21.5	2.5	0.30	1.25	0.9
Pachyrhizus erosus Jícama	89.0	7.89	1.78	0.00	1.03	0.3
Maranta arundinacea Sagu	57.2	37.07	2.43	0.13	1.91	1.3

Table 5.5 Vitamins and minerals of 'camotes' (mg/g dry weigth)

Especie	carotene	Vit C	Thiamine	Riboflavin	Niacin	Ca	P	Fe
Ipomoea batatas Camote amarillo	2.7	27.2	0.10	0.04	0.70	43.0	46.0	2.40
Ipomoea batatas Camote blanco	0.04	25.4	0.09	0.04	0.44	66.0	36.0	2.70
Manihot esculenta Guacamote	–	35.0	–	–	–	–	–	–
Xanthosoma sp. Pisis, Barbarón	2.0	96.0	0.06	0.02	1.00	–	–	–
Pachyrhizus erosus Jícama	0.00	30.9	0.02	0.07	0.21	30.0	8.0	1.30
Maranta arundinacea Sagu	0.00	8.9	0.08	0.03	0.66	20.0	24.3	3.20

These plant structures are of high value as foodstuffs worldwide as a source of energy [78], but in Mexico are rather consumed as an accessory or complementary foodstuff, maybe due to the presence of maize as the basic supplier of energy for the human population.

Consumption of camotes has a long tradition in the country. Francisco Hernández mentions numerous edible roots, and Bernardino de Sahagún in his sixteenth century writing known as the Florentine Codex describes them as follows (Eleventh book, paragraph nine):

> "*On the edible roots:*
>
> *The roots of the tree called **Quauhcamotli** are edible as was said. There are other roots good to eat that are formed like turnips underground, which are called **Camotl.** These are yams from the land. Eaten cooked, raw, and roasted. There are other roots that are eaten raw, which are called **Xicamas**. They are soft and white and well quench thirst. There are other roots that are also eaten that are called **Cimatl**. They are eaten cooked and if eaten raw are harmful. They are naturally white, when cooked becoming yellow.*"

Camote, *Ipomoea batatas* (L.) Lam. Convolvulaceae

Camote, *Ipomoea batatas*, is a species native to Mesoamerica that due to its intolerance to frosts is currently cultivated in 25 Mexican states in the tropical and subtropical regions of the country. Camote has a high agrodiversity in Mexico, the producers distinguishing varieties based on the color of the periderm and the flesh of the tubers, which may be red, purple, yellow, orange, or white.

Camotes are cultivated for the market and for self-supply and, despite its potential as an energetic food due to its high content of carbohydrates, it is a supplementary foodstuff consumed in sweetened preparations as a dessert or candy. Among the emblematic candies in Mexico are the camotes from Puebla, as is characteristic in several cities to see camotes being baked and sold in specially equipped carts. In the Bajío region, camote is consumed sweetened by boiling it in pure unrefined sugar (*piloncillo*), or baked in dome ovens and sweetened with the syrup secreted by the baked tubers.

The use of camote as food was common since Prehispanic times, as documented by Bernardino de Sahagún in the sixteenth century [77]. Its use in Mexico persists until the present, but it does not reach the importance observed in other countries as a source of carbohydrates.

Cimat, *Phaseolus coccineus* L. Leguminosae

The thickened roots of the frijol ayocote or botil, *Phaseolus coccineus* are known as *cimat*. This species of bean is cultivated in the temperate highlands as a monoculture in the plateau region of Puebla and Tlaxcala, Durango, Zacatecas, and Chihuahua, or in association with maize, which is the common form of cultivation in southern Mexico. The growth habit of *P. coccineus* is highly variable, while always being determinate, varying from sub-shrubs to vines with over 6 m long guides, the latter forms being used for obtaining the roots for consumption. The use of cimat as food has been documented in several ethnic groups from Chiapas, Puebla, Veracruz, and Hidalgo; however, always being well cooked by boiling for up to 12 h, or otherwise it may cause gastric problems such as vomiting and diarrhea.

Chayoteste or Chinchayote, *Sechium edule* (Jacq.) Sw. Cucurbitaceae

Chayoteste and *chinchayote* are names given to the root of the *chayote* or *espinoso*, *Sechium edule*. The species is mainly cultivated for its fruit, of which varieties for exportation have recently been selected. However, in several regions of Mexico the roots are also consumed, in some places the roots exceeding the economic importance of the fruit. Such is the case of the Sierra Norte de Puebla where a box containing approximately 25 kg of fruits is sold for $10.00, while a box of chayoteste can cost up to $600.00. In this region, it is common to see the roots offered in local markets during the first months of the year, where it is retailed for local consumption or sold in bulk for being sold in the cities of Puebla and Mexico City.

The root is eaten cooked in beef or chicken broths, or in cakes battered with eggs and filled with cheese.

Pezuña de burro, *Maranttia weinmanniifolia* Liebm. Marattiaceae and camote de pesma, *Lophosoria quadripinnata* (J.F. Gmel.) C.Chr. in Skottsb. Lophosoriaceae

Maranttia weinmanniifolia and *Lophosoria quadripinnata* are fern species having edible rhizomes. In Mexico, *M. weinmanniifolia* is distributed in cloud and tropical forests in the states of Querétaro, Hidalgo, Jalisco, Puebla, Veracruz, and Oaxaca, and is known as *pezuña de burro* (donkey's hoof), *papa de monte* (mountain potato) or *maíz de monte* (mountain maize) [79]. The use as food of the rhizome (*camote*) of the pezuña de burro is reported from Puebla, Veracruz, and Oaxaca, where it is prepared roasted or boiled.

Lophosoria quadripinnata is distributed in eastern and southern Mexico along stream margins and humid ravines of cloud forests [80]. In northern Puebla, the plant is called *pesma* and its rhizomes were formerly mixed with nixtamalized maize dough to be used to make tortillas as an emergency foodstuff when maize crops failed. At present people know such use, but it is practically never applied due to better communications allowing for accessing other markets in times of maize scarcity.

Papitas güeras o papas de monte. *Solanum cardiophyllum* Lindl. Solanaceae

It is a species native from central Mexico, where it is gathered for its consumption and commercialized at the local and regional levels, supplementing the household income from crops and grazing animals. Mainly gathered in San Luis Potosí, Aguascalientes, Zacatecas, Guanajuato, and Jalisco.

The potatoes are gathered in the milpa, their recollection being easy because it only requires manual picking once the plots have been placed left follow in preparation for the next cropping cycle. Alternatively, men, women, and children use hoes, peaks, or shovels to dig up the tubers that are sold in markets. It is thus an agricultural weed whose tubers are cropped for self-consumption, and sold by local people, particularly during Lent, when it reaches high price due to the high demand and low offer [81].

Quelites

Quelites—derived from the Nahuatl term, *quilitl*, meaning edible herb, with equivalents in other indigenous languages (Table 5.6) occupy an important position among edible plants, presently with over 250 registered species distributed throughout the country [82].

Many of the more amply spread and consumed quelites are crop weeds in a diversity of agroecosystems—such as *milpa* (corn-bean-squash field), *chilar* (chili pepper field), *frijolar* (bean field), *cafetal* (coffee groves), and rural dooryards—with variable intensities of management going from gathering of wild plants or weeds to monoculture, and side by side with domesticated plants [16, 83–88].

In the case of begonias collected in natural forests in the Sierra Norte de Puebla, gatherers plant leaf blades in an effort to increase density by vegetative propagation in situ, thus making use of the plants' capacity for natural regeneration [89, 90].

Some quelites such as *papalo* and *pipicha* (*Porophyllum* spp.), *verdolaga* (*Portulaca oleracea*), *xual* (*Chenopodium berlandieri*), *chepiles* (*Crotalaria pumila*), *alaches* (*Anoda cristata*), *romerito* (*Suaeda nigra*), *quintonil* (*Amaranthus spp.*), turnip (*Brassica rapa*), and mustard (*B. juncea*) are produced under monoculture systems developed by the initiative of cultivators, who use their own technology developed by empirical experimentation [87, 88, 91–94].

Table 5.6 Quelites name in different native languages

ntiyia	mazateco
yiwa o yube	mixteco
quilitl o quilit	náhuatl y náhuat
k'ani	ñahñu
xakua	purépecha
guilibá	rarámuri
akw'aal	tenek
ivagi	tepehuan
kaka	totonaco
bok?itah	tzeltal
itaj	tzotzil

Table 5.7 Proximal analysis of quelites (% dry weigth)

Especie	moisture	ash	E.E	protein	fiber	CH
Amaranthus cruentus	4.7	25.0	0.9	24.2	11.2	34.0
A. hypochondriacus (tough)	6.9	19.9	4.8	19.1	14.0	35.3
A. hypochondriacus (tender)	6.1	25.4	2.9	24.3	14.1	27.2
Begonia barkerii	2.5	18.2	1.4	11.7	20.2	46.0
Brassica rapa	7.3	14.3	3.0	32.0	15.3	28.1
Cyclanthera langaei	5.8	20.2	3.2	20.4	24.0	26.4
C. ribiflora	5.6	25.5	2.1	16.9	33.2	16.7
Chenopodium berlandieri	4.0	28.4	1.9	24.6	11.3	29.8
Erythrina americana	4.6	9.4	1.8	34.8	16.1	33.3
E. caribaea	4.7	10.1	2.0	27.9	19.1	36.2
Jaltomata procumbens	4.0	15.2	2.4	30.8	13.2	34.4
Persea americana	5.0	6.2	2.4	18.9	17.9	49.6
Phaseolus dumosus (foliage)	4.3	8.3	2.5	34.4	13.3	37.2
P. dumosus (seedling)	2.6	13.7	1.4	27.8	17.1	37.4
Phytolacca icosandra	4.2	20.1	1.7	24.9	13.8	35.3
Piper auritum	4.4	12.1	2.1	29.8	11.9	39.7
Pisum sativum	3.3	10.3	3.5	46.6	14.2	22.1
Porophyllum macrocephalum	4.0	14.0	2.2	23.1	16.0	40.7
Rumex crispus	8.3	17.8	3.1	22.5	14.7	33.6
Sechium edule	4.3	14.7	1.2	33.4	18.2	28.2
Solanum americanum	3.3	14.1	1.5	27.9	18.5	34.7
Tinantia erecta	4.1	17.9	1.8	22.8	15.7	37.7
Xanthosoma robustum	4.6	12.2	8.6	30.4	17.8	26.4

In localities of the Sierra Norte de Puebla quelites are considered not to represent a meaningful competition with crops, at least during some phases of their development [86], a conception that is supported by the works of Chacon and Glissman [95], Kohashi and Flores [96], Kahl [97], and Castro, Basurto and Martínez [98], which show that some species of quelites growing as crop weeds do not necessarily compete with crops nor they diminish their yields, instead providing an extra crop to traditional agricultural systems.

The history of quelites as food goes back over 500 years, the names and uses of many of their species remaining unaltered since then [73, 99, 100], currently remaining to be consumed as daily foodstuffs, mostly by people from rural areas of Mexico [101].

Quelites are supplementary foods, although in some regions and during some seasons they are an important part of the diet, becoming mainstays together with maize tortillas and any of the variety of hot sauces [48, 84, 85, 102, 103]. Quelites contribute mostly vitamins and minerals, but some provide a high ratio of protein content on a dry weight basis (Table 5.7).

Species used as quelites belong to 121 genera from 46 plant families, the largest number of species (67 or 27 % of all currently used species of quelite) being concentrated in the families Leguminosae, Asteraceae, and Begoniaceae; on the opposite range, 12 families include only one species of quelite (Fig. 5.10).

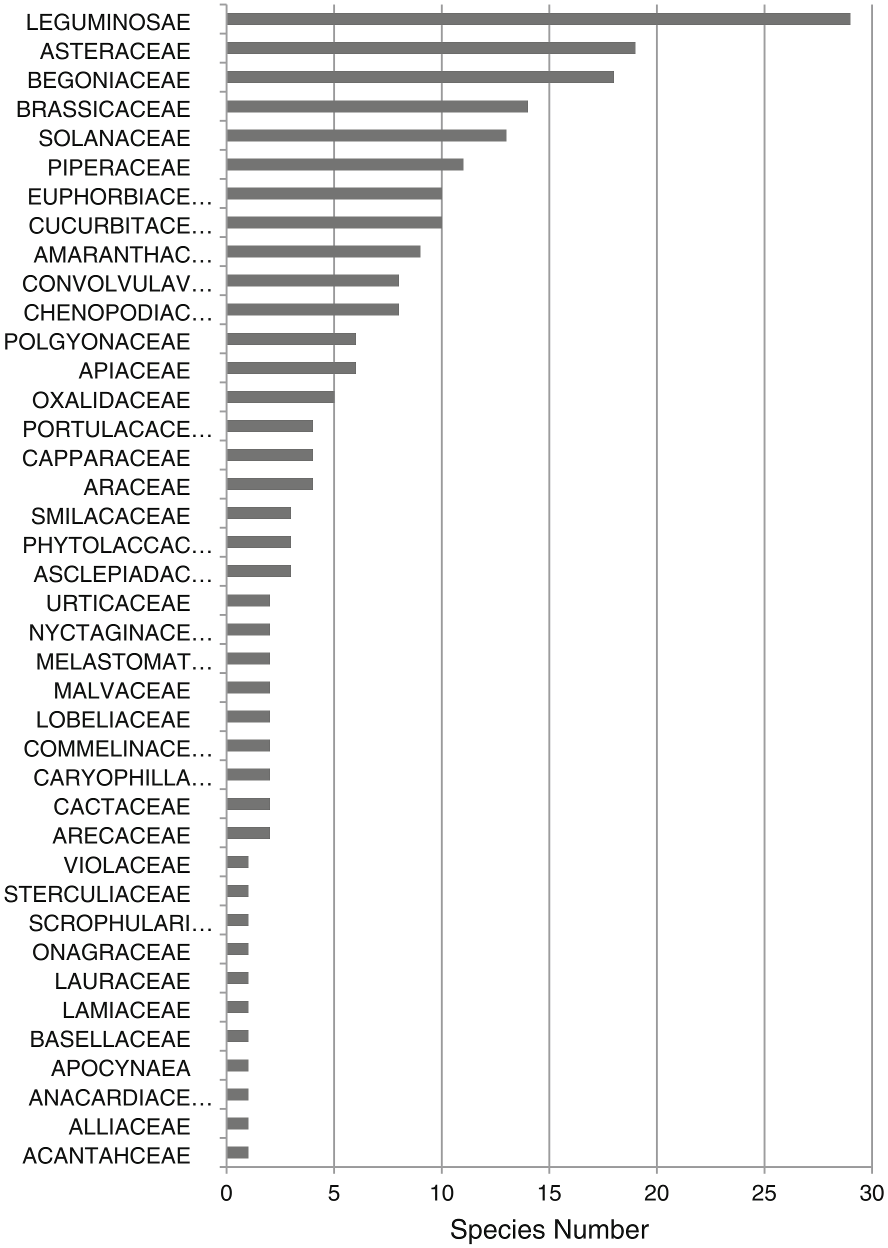

Fig. 5.10 Quelites species per family

Chepiles and *chipilines*, *Crotalaria* spp., Leguminosae

According to data in the National Herbarium (MEXU), 29 species of *Crotalaria* are represented in Mexico, six of which (*C. acapulcensis* Hook. & Arn., *C. cajanifolia* Kunth, *C. eriocarpa* Benth., *C. longirostrata* Hook. & Arn., *C. pumila* Ort., and *C. sagittalis* L.) are used as quelites in the states of Chiapas, Oaxaca, Guerrero, Michoacán, Morelos, Veracruz, Puebla, and Hidalgo, where they are named *chepil*, *chipil*, or *chipilin* and eaten in soups and tamales.

Chepiles are usually gathered in crop fields or other areas disturbed by human activity, but in some locations in the Central Valleys of Oaxaca the chepil *C. pumila* is also produced in monoculture.

Papalos, and *Pipicha*, *Porophyllum* spp., Asteraceae

At least six species of *Porophyllum* are used as quelite in Mexico—commonly named *papaloquelite*, *hierba del venado*, *tlapanche*, *chepiche*, or *pipicha*—to accompany raw foods, or cooked with beans for flavoring. Mainly used in the states of Guerrero, Puebla, Oaxaca, Veracruz, Morelos, and Guanajuato [94, 104]. The plants are gathered, favored as crop weeds, or cultivated in a number of agricultural systems both with other crop species as in monoculture [92, 94].

Agrios or *Xocoyolis*, *Begonia* spp., Begoniaceae

At least 18 species of *Begonia* are reported to be consumed as quelites in Mexico: *B. barkerii, B. calderonii, B. caroliniifolia, B. extranea, B. franconis, B. fusca, B. glabra, B. gracilis, B. heracleifolia, B. incarnata, B. manicata, B. monophylla, B. nelumbiifolia, B. pedata, B. plebeja, B. pustulata, B. rex*, and *B. thiemei* [89, 90, 105], the edible parts are leaves and petioles that are appreciated for their sour flavor. Begonia leaves are consumed raw with other foodstuffs, cooked with chili-peppered beans, and in sauces substituting tomatoes (Fig. 5.11).

Quintoniles, *Amaranthus* spp., Amaranthaceae

The *quintoniles* are more commonly consumed quelites in several regions of Mexico, including at least 12 species of *Amaranthus*: *A. hybridus* L., *A. retroflexus* L., *A. palmeri* S. Watts, *A. powellii* S. Wats., *A. dubius* Mart. ex Thell., and *A. spinosus* L. All these are weeds on roadsides and crop fields. Compared with the grain producing varieties of *Amaranthus* spp., quintoniles are smaller, have smaller flowers and fruits, and their seeds have a darker color.

Leaves of *A. hybridus* L., *A. hypochondriacus* L., and *A. cruentus* L. are used in the Sierra Norte de Puebla region. Plants are favored or induced in the milpas by intentionally casting their seeds in recently opened crop fields [88].

Fig. 5.11 *Begonia* barkeri Knowles & Westc. Photo: Francisco Basurto

Fig. 5.12 Quintoniles. *Amaranthus hypochondriacus* L. Photo: Cristina Mapes

Amaranths are collected in milpa, chilar, frijolar, and dooryard agroecosystems, as well as in vegetable fields. Seasons for production of amaranths vary depending on the agricultural calendar, itself being determined by cultural and environmental conditions.

In the Sierra Norte de Puebla, quintoniles are highly appreciated as food, having high demand among mestizos and indigenous people. They are sold in local markets, their price varying according to the season of the year, and whether seedlings or sprouts are being sold (Fig. 5.12).

Quintonil plants sprout readily because people continuously cut their apical portions. Broth is made exclusively of seedlings, after that stage, the leaves are boiled, drained, and fried. Once in flower, leaves are not any more consumed.

Mafafa or paxnikak, *Xanthosoma robustum* Schott. and *X. violaceum* Schott., Araceae

The *mafafa* or *paxnikak* are two species of *Xanthosoma* used for food in the Sierra Norte de Puebla to prepare the dish called the plant paxnikak, in Totonac meaning pig quelite. Preparation of paxnikak requires knowledge, given that as many other plants in the family Araceae, they are rich in calcium oxalate, a substance causing irritation and inflammation of mucous tissue that can cause severe problems. To avoid the oxalates, only tender leaf blades—veins or nerves being discarded—are boiled in water constantly moved to disaggregate the paxnikak leaves with the addition of *xocoyoli*, *piñoncillo* or sesame, green chili pepper, and avocado leaves. Paxnikak is consumed with maize tortillas [98].

Mafafa plants are tolerated or protected in humid and shaded sites and are also seen under incipient cultivation in dooryards and coffee groves. Their roots are also edible.

Drinks and Fermented Foods

In the following sections, we summarize Herrera's [106] excellent review.

Pulque

Pulque is the product of fermentation of *aguamiel*, which is the sugary sap of certain agave species (*maguey*) called *magueyes pulqueros* (pulque producing maguey), mainly *A. salmiana* Otto ex Salm-Dick var. *salmiana* (*maguey manso*, tame maguey), and *A. atrovirens* var. *mirabilis* (Trel.) Gentry (*maguey cenizo*, ash-colored maguey). The former is the most frequently cultivated species of maguey in the states of the Mesa Central (southern Mexican Plateau) for extracting aguamiel, while the latter is only planted for that purpose in the highlands of Mexico, where it also grows wild and, therefore, is sometimes called *maguey de cumbre* (hilltop maguey).

Aztecs called this drink *iztacoctli* (from *iztac*, white and *octli*, fermented alcoholic drink) or *metoctli* (from *metl*, maguey and *octli*). The word pulque is derived from the Nahuatl *poliuhqui*, meaning decomposed or rotten. The word was transmitted to Spanish conquerors by Indians and it referred to foul-smelling pulque fermented beyond the conditions for favorable bacteria and yeasts, and undergoing decay by the activity of decomposer microorganisms. While recently extracted aguamiel is rapidly converted to a mild, sweet pulque called *tlachique* (from Nahuatl *tlachiqui* to scrape something), as fermentation advances, pulque goes through several stages of taste, reaching to a strong but still agreeable flavor, afterwards becoming repugnant.

In order to flavor pulque or to mask its unpleasant flavor, fruits (prickle pear or *tuna*, cantaloupe, watermelon, tomato), ground seeds (pecan, pine nut), vegetables (celery), and cereals (oats) are added to prepare pulque *curado* (from Spanish, *curado*, cured). All these modifications produce noticeable changes in the microbial composition of pulque.

Pulque is a drink with considerable ethnobiological importance, as shown by the existence in Prehispanic Mexico of the deities involved in the cults of maguey and pulque, in particular the goddess *Mayahuel* (meaning about, or concerning, maguey, derived from the Nahuatl *metl*, maguey and *yaual*, about) and her brothers the *Centzontotochtin* or 400 rabbits (from Nahuatl *centzotlin,* 400 and *totochtin*, rabbits). Despite that the cult to pulque was lost, and that in recent years its consumption has been lowered by its displacement by beer and other drinks, in rural areas of central Mexico it remains to be an important ingredient of the diet of indigenous people and mestizos.

Low-income people consume pulque not only as an alcoholic beverage, but also as a dietary supplement due to its high content of protein and B-complex vitamins that are provided by the microorganisms developing in the beverage, particularly by yeasts.

The most abundant yeast in pulque is the same as in bread and beer, *Saccharomyces cerevisiae* Meyen ex Hansen, but other species from the genera *Candida, Kloeckera*, *Rhodotorula*, and *Torulopsis* also develop in pulque.

Among bacteria, the more constant are *Lactobacillus buchneri*, *Lanoconostoc mesenteroides*, L. *dextranicum*, and *Zymomonas mobilis*. The presence of these microorganisms that are considered to improve the intestinal flora and avoid the proliferation of pathogenic and decomposer bacteria confers curative properties to pulque, and some preparations made from pulque are recommended for treating peptic ulcers and gastritis.

Colonche

Colonche is a fermented drink prepared by fermenting the juice of several species of prickly pear fruits (*tunas*), in particular of *Opuntia streptacantha* Lem (*tuna Cardona*), *O. orbiculata* Salm-Dyck (*tuna pintadera*), and *O. leuptotricha* D. C. (*duraznillo*). The drink is traditionally consumed by indigenous people from Chihuahua and Sonora, especially the Rarámuri (Tarahumara) and the Yaqui, and by mestizos from Zacatecas, San Luis Potosí, Querétaro, Guanajuato, and Hidalgo; but only during the season of the year in which prickly pears produce their fruits.

Colonche is generally prepared by women who crush the tunas to obtain the juice, boil it, allow it to cool, add old colonche or tibicos (gelatinous masses made up of dextran and yeasts developing on the cladodes of prickly pear plants) as a starter of fermentation, and allow for fermentation following an antique procedure avoiding reaching a stage in which the product becomes acidified.

Aztecs called this beverage *nochoctli* (from Nahuatl, *nochtli*, tuna and *octli*, fermented alcoholic drink), while the word colonche is derived from the Nahuatl *coloa*, to bend, because of its inebriating effect.

The yeasts responsible for the fermentation of colonche belong to the genera *Saccharomyces* and *Candida*, in particular, *S. cerevisiae* and *C. valida*. The bacteria present in colonche have not been identified.

Tepache

Tepache is a popular drink with Prehispanic roots, although it was then prepared from maize and at present it is made from fruits such as pineapple, apple, and orange. It has been suggested that the word *tepache* is derived from the Nahautl *tepochoa*, from *tetl*, stone and *pochoa* to grind or press something with a stone.

Among the identified microorganisms contributing to the fermentation of tepache are the bacteria *Bacillus megaterium* and *B. subtilis*, and the yeasts *Saccharomyces cerevisiae*, *Pichia membranaefaciens*, *Candida boidinii*, and *C. incospicua*.

Tesgüino

Tesgüino is mainly consumed in Chihuahua by the Rarámuri (Tarahumara), in Sonora and Chihuahua by the Makurawe (Guarijíos), in Durango by the Tepehuan, and in Jalisco and Nayarit by the Wixáricas (Huichol). The name of the drink is derived from the Nahuatl *tecuini*, to beat, due to its alcoholic effect.

Several kinds of tesgüino are made depending on the ingredients with which it is prepared. The most common tesgüino is made with maize kernels and is named *batári*, when made with wheat it is called *suguíki*, if made with sorghum or agave leaves it is simply called tesgüino, and if made with maize canes it is named *paciki* or *mabatán*.

Tesgüino prepared from moistened maize kernels germinated in the darkness can be considered as a maize beer. The grains are afterwards ground in a *metate* (a mealing stone) and are boiled in water to obtain *atole* (maize gruel). The atole is strained and mixed with catalyzers that can either be bark, stems, and roots of several plants, and leaves of oaks or other plants. The catalyzers accelerate the process of fermentation either because they contain fermenting microorganisms, provide growth factors or vitamins needed for microorganisms, or selectively regulate growth of different populations of microorganisms.

In occasions, fortifiers are used instead of catalyzers, for example, hallucinogenic plants such as peyote. The fermentation is maintained for a few hours or days and it is consumed without additional treatment. Several species of yeasts and bacteria develop in tesgüino.

Once fermented, tesgüino is consumed unfiltered, is not pasteurized, nor is it pulverized because of which it retains the living microorganisms involved in fermentation in full activity, together with substances metabolized by them, and the residues of the plant materials used for its production.

Tesgüino has a high ethnobiological importance because of the *tesgüinadas* celebrated around the large *tesgüinera* pot containing the beverage, in which some individuals may get drunk due to its alcoholic content. However, in general, tesgüino is a mean for formal celebration of relevant events in the lives of certain indigenous peoples, in particular, of the Rarámuri (Tarahumara).

Besides an alcoholic drink, tesgüino is a dietary supplement and source of calories for the indigenous peoples consuming it at present.

Pozol

Pozol is fermented from maize dough (solid fermentation) and is used as a basic staple in the diet of indigenous peoples from southeast Mexico, in particular from Chiapas (Lacandon, Chamula or Tzotzil, Tzeltal, Chol, Mames, and Zoque), Tabasco (Chontal and Chol), Campeche, Yucatán and Quintana Roo (Mayan), and Oaxaca (Zapotec). Sometimes, it is ingested as the only foodstuff during one or several days during the long workdays in the field or in the forest, simply prepared by suspending in water a portion of pozol.

The word *pozol* is derived from the Nahuatl *pozolli*, meaning foamy. However, since it is the product off an essentially lactic, solid fermentation, gases, and alcohol are not produced as in liquid fermentation, the name referring to the masses of fermented dough rather than to the effects of fermentation.

As other indigenous fermented products, pozol has a high ethnobiological relevance because since Prehispanic times it was prepared not only for food, but also as medicine for ailments such as diarrhea, and as a cataplasm for superficial skin infections. It also is important in ceremonies; the Maya used it as an offering to the gods in agricultural rituals, in particular of maize cultivation.

There are several ways to prepare pozol; in general, it is made with maize kernels boiled with lime to produce *nixtamal*, which are later ground to obtain dough that is molded as large or small balls, either spherical or elongated. Dough balls are wrapped, generally in banana leaves, and fermented according to the taste of indigenous groups either for several days or, if moldy pozol is desired, for several weeks. In Tabasco, pozol is prepared mixing cocoa grains, a modality called *chorote*.

The predominant microorganisms in pozol are lactic bacteria and the presence of nitrogen fixing bacteria is noticeable, which favors protein synthesis that enhances the nutritional value of the fermented product relative to unfermented maize dough, explaining the preference for pozol as food.

Mezcal, Tequila, Bacanora, and Sotol

Tequila, bacanora, and sotol are distilled beverages that can be considered as varieties of mescal. Etymologically, the word *mescal*, or *mescal*, derived from the Nahuatl *metl*, maguey and *ixcalli*, boiled, meaning boiled maguey. The beverage is prepared with the stems and leaves of several species of the genus *Agave*, parts respectively called *cabezas* (heads) or *piñas* (pines), and *pencas*. Roasted and boiled agave stems and leaves are fermented, and afterwards the alcoholic beverage is obtained by distillation in rudimentary stills, although currently also in modern distillation apparatuses (mainly tequila).

Bacanora or *mescal bacanora* is the traditional alcoholic drink of Sonora, its name being derived from the town of Bacanora in the eastern part of the state. It is prepared by fermentation and distillation of the crushed, boiled stems and leaf bases of *Agave angustifolia*, called *maguey de mescal* or *maguey bacanora*.

Sotol is the traditional alcoholic beverage of Chihuahua, although it is also consumed in Durango, Coahuila, and Zacatecas. It is prepared as other mezcales, but using plant material of species of the genus *Dasylirion*, whose common name is *palmilla* or *maguey de sotol*. As in traditional mescal, rudimentary stills are used for distilling sotol.

Chocolate and Cocoa. *Theobroma cacao* L. Malvaceae

Cacao (cocoa) is the name given to *Theobroma cacao* L., which is the tree that produces the raw material for obtaining chocolate. Despite that, the words chocolate and cocoa are widespread throughout the world, together with other variants in several languages; there is no consensus regarding their origin or meaning.

For some authors, the word cocoa is derived from the Mayan *cacau* composed of *cac*, red and *cau*, strength or fire [107], while others consider cocoa to be derived from the Mije-Zoquean word *kakawa* and to be widespread in Mesoamerica [108]. The word chocolate is derived from the Nahuatl *xoloatl*, meaning foamy water, a word that according to Kaufman and Justeson [108] appeared until the late sixteenth century, while in the early chronicles the word *kakawatl*, meaning cocoa water, is used to describe the drink made with cocoa, water, and honey.

The genus *Theobroma* includes 20–22 species and its center of diversity is in the Amazon Basin, with only two species distributed north of Costa Rica and reaching southeast Mexico: *T. cacao* and *T. bicolor* [107, 109, 110].

Two subspecies are recognized of *T. cacao*: ssp. *cacao*, of better quality and corresponding to the *criollo* cocoa trees native of Mesoamerica, and ssp. *cphaerocarpum*, corresponding to the foreign cacao trees from South America. A third agronomic category contains the Trinitarian cacao trees, considered to be hybrids of the former two subspecies.

Cocoa is known to be cultivated in Mexico since at least 3000 years. Mesoamerican cultures used the seeds as coin because of which drinking chocolate was a privilege reserved for the elites. Numerous flavoring and aromatizing additives were added to chocolate, including achiote (*Bixa oreyana* L.), vanilla (*Vanilla planifolia* Andrews), chili pepper (*Capsicum annum* L.) honey, ground seeds of ceiba (*Ceiba pentandra* Gaertn) or of mamey (*Pouteria sapota* [Jacq.] H.E. Moore & Stearn), allspice (*Pimenta dioica* [L.] Merr.), and flowers such as those from *Cymbopetalum penduliflorum* (Dunal) Baill., *Piper sanctum* (Miq.) Schltdl., *Quararibea funebris* (La Llave) Vischer, *Magnolia dealbata* Zucc., and *Magnolia mexicana* DC [111].

At present, cocoa is object of an important world industry of which Mexico has little participation, but several traditional beverages made from cocoa and most likely of Prehispanic origin are preserved in the country. Such are definitively the cases of the *tejate* and *chocolate-atole* from the Central Valleys of Oaxaca; the *bupu* from Istmo; the *pozol chorote* from Tabasco; the *pozol* and *tascalate* from Chiapas; the *popo* from Veracruz and the *tanchuca* from Yucatán y Tabasco. All these drinks, all beverages, except popo, combine cocoa with corn.

Tejate is made with toasted corn, cocoa, mamey seed and flavored with rosita de cacao *Quararibea funebris*, everything ground to form a dough that is beaten by hand in a pot with water to form a thick foam.

Chocolate-atole is a drink that combines corn gruel with foam made with cocoa seeds; the cocoa are prepared burying wet until it acquires a white color and mealy consistency; this white foam is served combined with corn gruel to drink; similar to the above is the bupu of the Tehuantepec Isthmus Zapotec, also being a foam is drank with maize atole, but prepared with roasted, ground cocoa, added with molasses, cinnamon, and flor de mayo (may flower; *Plumeria rubra*);

The *pozol chorote* from Tabasco, the *pozol* and *tascalate* from Chiapas, the *popo* from Veracruz, and the *tanchuca* from Yucatán and Tabasco [112]. All these afore-mentioned beverages except the *popo* are prepared combining maize and cocoa. The *tejate* is prepared with roasted maize, cocoa, and mamey seeds aromatized with *Rosita de cacao.* The *atole de cacao blanco* is a froth made with cocoa seeds fermented by burying them until they acquire a white color, from which the beverage receives its name. *Pozol* is made with fermented nixtamalized maize dough to which ground cocoa is added. The *tanchuca* is a beverage prepared with maize spiced with anise and chocolate. The *tascalate* is made with roasted maize ground with cacao, achiote, and a small amount of cinnamon, the ground mixture being drunk after dilution in water.

Edible Flowers

Flowers used as food in Mexico add up to over 100 native species representing at least 49 genera in 25 plant families, among which Agavaceae, Leguminosae, Arecaceae, Cactaceae, and Cucurbitacea contain the largest number of species (Table 5.8).

The use of flowers as food is widely distributed throughout the country, from the northern Raramuri or Pima to several peoples in Tabasco and Chiapas [39, 113–117]. In the arid zones, most eaten flowers are from the agave and cactus families, while in humid and warm climates the inflorescences of palms are consumed.

Flowers can be eaten as buds or at anthesis, a stage in which stamens or the ovary is frequently removed to avoid bitter flavors.

Being edible flowers mostly from wild plants, they are seasonal food items consumed only during particular seasons of the year, in contrast to cultivated plants available during a longer part of the year. A single exception is the *huauzontle*

Table 5.8 Major Families, Genera and Species of edible flowers

Family	Genus	No. species
Agavaceae	**5**	**23**
	Agave	14
	Beschorneria	1
	Dasylirion	2
	Nolina	1
	Yucca	5
Leguminosae	**9**	**23**
	Bahuinia	1
	Canavalia	1
	Cercidium	2
	Cercis	1
	Diphysa	1
	Erythrina	12
	Gliricidia	1
	Leucaena	1
	Phaseolus	3
Cactaceae	**8**	**12**
	Carnegia	1
	Echinocereus	1
	Ferocactus	5
	Lemairocereus	1
	Myrtillocactus	1
	Neobouxbamia	1
	Nopalea	1
	Selenicereus	1
Arecaceae	**3**	**5**
	Astrocaryum	1
	Chamaedorea	3 especies
	Scheelea	1 especie
Cucurbitaceae	**1 género**	**4 especies**
	Cucurbita	4 especies

Chenopodium berlandieri Moq. ssp. *nuttaliae* (Saff.) H. D. Wilson & Heiser (Fig. 5.13) that is expressly cultivated for consumption of its inflorescences. Other cultivated or domesticated plants with flowers used as accessory products of the main crop are the *ayocote* or *botil*, the squashes, and the pulque producing species of maguey (*Agave* spp.).

Flowers are seasonally consumed and are complementary foodstuffs, although they can sometimes be the main ingredient of the day meal, always accompanied by maize tortillas; in other cases, flowers are used as emergency food in times of shortage, as are the flowers of *Quercus albocincta* Trel., or those of *Fraxinus pappillosa* Lingelshein among the Raramuri [114], or—in the Sierra Norte de Puebla—the

Fig. 5.13 Huazontle. *Chenopodium berlandieri* Moq. ssp. *nuttalliae* (Saff.) H.D. Wilson & Heiser. Photo: Francisco Basurto

Table 5.9 Proximal analysis of Agave flowers (% dry weigth).

Species	moisture	ash	E E	protein	fiber	CH
A. mapisaga maguey xamini	9.08	5.46	4.64	11.06	17.10	52.68
A. salmiana maguey palmilla	8.87	7.68	4.98	19.57	14.03	44.87
A. americana maguey blanco	8.83	7.15	5.74	13.84	15.13	49.31

maize spikes (masculine flowers) that are mixed with *nixtamal* to increase the volume when grain is scarce [103]. In this same region, maize spikes are also prepared with brown sugar (*panela* or *piloncillo*) and eaten as sweets.

While most edible flower species are either wild or crop weeds being chiefly gathered, about 40 % of these species are object of people's protection or cultivation, some even being domesticated as in the case of the flowers of the ayocote bean (*Phaseolus coccineus* L.), and of the squash flowers (*Cucurbita* spp.)

In the state of San Luis Potosí, the flower buds of wild *biznaga colorada Ferocactus haematacanthus* (Monv.) Berg. (locally named *cabuches*) are preserved, and locally sold in jars [118].

Flowers provide mostly vitamins and minerals to the human diet, due to their high content of water resulting in very low contents of proteins and carbohydrates (Tables 5.9 and 5.10).

Table 5.10 Vitamins and minerals of *A. salmiana* flowers. (mg/g dry weigth)

	Fe	Ca	Mg	Vit a	VitB1	VitB2	VitB3
A. salmiana maguey palmilla	8.92	312.69	270.44	126.39	0.19	0.19	5.68

Several of the species with edible flowers belong to genera—or families—containing toxic substances such as *Agave*, *Erythrina*, *Plumeria*, *Quercus*, and *Yucca*, in which cases their preparation involves heat that inactivates the toxins [119]. Consumption of flowers at early stages of development, or elimination of some structures such as stamens or ovaries, is part of the strategies aimed at elimination of toxic substances together with pretreatment of flowers in lime water ($CaCO_3$) or *tequesquite* (Na_2CO_3), and elimination of the cooking water.

Agaves and Yuccas

The flowers of *Agave*—known as *cacayas*, *bayusa*, *golumbos*, *dembos*, or *manitas de maguey*—are sold in markets and can be prepared either with eggs, or fried with some onion and green chili pepper. The flower stalk or scape (*quiote*) of *Agave* is also eaten after being boiled or cooked in underground ovens.

Flowers of *Yucca* are known as *chochas*, *flor de palmo*, or *flor de izote*, and are either eaten as buds, or the ovaries are removed to avoid the bitter taste from the high content of saponins in the genus.

Legumes

The genus of Leguminosae with more species with edible flowers is *Erythrina* with 30 species in Mexico, of which the flowers of 12 are eaten by people, and known as *colorines*, *gasparitos*, or *tzompantles*; the genus has a high content of alkaloids, but the alkaloid concentration in flowers is very low allowing for their safe consumption. The flowers are frequently eaten as lent food—*de vigilia*, or *de Cuaresma*.

Traditionally, flowers are boiled in water and mixed with egg. They are also cooked in soups or added to salads. Flowers are sold in several markets of Mexico [120].

Flowers of ayocote bean (*Phaseolus coccineus* L.) are highly appreciated in some regions of Mexico eaten in soups, or incorporated to dough for tamales. This species easily escapes from cultivation and has a wild form (*P. coccineus formosus*); the flowers of cultivated, escaped, and wild populations are being equally gathered and consumed (Fig. 5.14).

The male flowers of the four Mesoamerican domesticated squashes (*Cucurbita* spp.) are used for food, people readily distinguish them from female flowers that are not eaten. The flowers of *Cucurbita pepo* L. and *C. moschata* Duchesne are frequently sold in markets, but those of *C. argyrosperma* K. Koch and *C. ficifolia* Bouché are only used for self-supply by gatherers, not reaching the local markets.

Fig. 5.14 Ayocote flower. *Phaseolus coccineus* L. Photo: Francisco Basurto

Conclusion

Despite that during the past decades the alimentary habits in Mexico have suffered drastic changes, not always towards their improvement; the numerous plant food resources of the country continue to be amply used. Such uses occur mainly in rural localities, but even in the large cities it is nowadays possible to find many edible plants, not always cultivated, which are consumed as a part of several culinary traditions of Mexico.

These plant food resources include basic foodstuffs that continue to be an essential part of the diets of Mexicans, such as maize, beans, and chili peppers, as well as many other plants used as seasonal foodstuffs during the periods of the year in which they are available, which supplement and vary the basic diet. The knowledge of these supplementary plant foodstuffs used as emergency food in times of scarcity has been conserved in Mexico.

In the context of selection and management of plant species by people, Mexican edible plants span throughout a continuum going from gathered wild plants to domesticated species, of which maize is an archetypal example.

Several stages can be distinguished along this continuum, such that plants can be considered as tolerated, favored, protected, or incipiently cultivated. The products of all these forms of management contribute to the diets of human populations, and, in many instances, can also play a prominent role as sources of monetary income for their producers.

Mexico is considered to be one of the few centers of origin of agriculture in the world, and the farmer peoples living in the country have an active and dynamic role in plant selection towards domestication. At present, there are many examples of rural populations, both indigenous and not indigenous, that are actively participating in processes of selection, conservation, and management of local plant genetic resources intended for their use as foodstuffs and for agricultural systems.

The knowledge generated and accumulated by people in Mexico goes beyond recognizing which plants are edible and which are not, and the ways for their production or gathering, but they also have developed and conserved a wealth of knowledge regarding the forms of uses and transformation of edible plants for their consumption. People have knowledge about methods for eliminating dangerous substances that make potentially toxic plants to become totally innocuous foodstuffs. These methods include dry and wet cooking, elimination of certain plant structures, consumption of plants during tender stages in which high concentrations of toxic components are absent, and fermentation. In this regard, nixtamalization deserves a special mention as a process by means of which nutrimental elements of maize are freed and enhanced, also achieving the adequate texture and plasticity needed for preparing products such as tortillas and tamales, which are inseparable from Mexican culinary traditions.

Selection of edible plants in Mexico has given origin to *manso* varieties, a term denoting forms lacking bitter or astringent flavors indicating the presence of toxic substances, as in the cases of the piñoncillo (*Jathropha curcas*) and yucca (*Manioth esculenta*).

The richness that is possible to record in Mexico of edible plant species, and of the knowledge of their uses and forms of preparation for human consumption, can be explained by two essential factors: the ample and unique biodiversity existing within the national territory, and the country's ample cultural wealth in the form of numerous peoples that have inhabited it until the present. The combination of these two factors makes Mexico a megadiverse and multicultural country.

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Chapter 6
Contemporary Maya Food System in the Lowlands of Northern Yucatan

Carmen Salazar, Daniel Zizumbo-Villarreal, Patricia Colunga-GarcíaMarín, and Stephen Brush

Abstract Lowland Maya culture can be traced back to around 1200–1000 BC in the lowlands of Belize. Their subsequent expansion and settlement in the northern portion of the Yucatan Peninsula was possible, thanks to the integration of three agricultural systems that originated in other dry tropical forests but were also adapted to the lithosol–cambisol physiographic and edaphic sequences of Yucatan: the Mesoamerican *milpa* (*Zea mays*—*Phaseolus* spp.—*Cucurbita* spp. complex), the South American *conuco* (*Manihot esculenta*—*Xanthosoma sagittifolium*—*Maranta arundinacea*—*Ipomoea batatas* complex), and the family garden based on native tree species but also on species introduced from other areas of Mesoamerica or from Central and South America. Hunting, gathering, and fishing complemented Mayan food production since their arrival in Yucatan. Various studies have enumerated Mayan foods and dietary patterns based on the *milpa* production system that has persisted since Pre-Columbian times. Nevertheless, we lack comparable reports on how the contemporary Maya structure their food system and the relative contribution of each of its various components. In order to address this need, we studied a traditional Maya community in northern Yucatan by making inventories of food dishes and drinks elaborated in the community and the origin of their ingredients. We found 74 food dishes and drinks primarily produced with ingredients produced locally in the *milpa*. 91.9 % of them included *Zea mays*, 29.7 % included *Cucurbita* spp., 12.1 % included *Phaseolus* spp., 12.5 % included *Capsicum* spp., 6.7 % included *Spondias*, and 5.4 % included *Cnidoscolus*. Although they have economic

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and nutritional importance, other production systems, such as the family garden, are clearly secondary to the *milpa* in contributing to Xocén's food supply. The culinary characteristics of different varieties of the cultivated species appear to have served as selective pressures for the generation and conservation of intraspecific diversity. Efforts to augment productivity of the *milpa* system through transforming it to a maize monoculture can yield significant changes to the food system with negative consequences to local nutrition, ecology, and culture.

Keywords Agro-biodiversity • Lowland Maya • Food system

Introduction

Plant domestication and the origins of agriculture in Mesoamerica date to 8900 years before present (BP), when at least maize (*Zea mays* L.) and squash (*Cucurbita* sp.) were domesticated [1, 2]. The beginning of agriculture represents an increase in knowledge, technology, and cultural practices relating to the preparation, consumption, and conservation of food. Cultivation and human selection improved the food quality of domesticated plants. Along with the development of agriculture, the Mesoamerican food system was established and likewise developed between 8900 and 4400 BP, comprised of maize, squash (*Cucurbita argyrosperma* Huber), beans (*Phaseolus vulgaris* L., *P. lunatus* L.), and chilli pepper (*Capsicum annuum* L.), conforming the so-called *milpa* system, and, depending of the Mesoamerican subregion, it included other species as tomato (*Solanum lycopersicum* L.), husk tomato or *tomatillo* (*Physalis phyladelphica* Lam.), hog plum (*Spondias purpurea* L.), avocado (*Persea americana* Mill.), and *chía* (*Hyptis suaveolens* L.) [3, 4].

Lowland Maya culture can be traced back to around 1200–1000 BC in the lowlands of Belize [5] where they had a maize-based system of food production along with squash, peppers, and several varieties of beans [6]. In the centuries that followed, they spread to the west and north and came to dominate an important part of Mesoamerica, developing one of Mesoamerica's and the New World's most extensive and successful cultures in terms of population size and cultural longevity and continuity [7]. It has been proposed that their cultural success in the northern portion of the Yucatan Peninsula was enabled by the productivity of the *milpa* in the ecological characteristics of that area, its ability to generate new landraces of the basic *milpa* species, and its integration of native species into this agri-food system [8].

The original Lowland Maya integrated two other production systems with the Mesoamerican *milpa* system: the *conuco* system from South America, based on an association of root and tuber crops (*Manihot esculenta* Crantz—*Xanthosoma sagittifolium* (L.) *Schott—Maranta arundinacea* L.—*Ipomoea batatas* L.), and the family home garden based on native shrub and tree species (e.g., *Brosimum alicastrum* Sw., *Carica papaya* L., *Cnidoscolus chayamansa* McVaugh; *Manilkara zapota* (L.) P. Royen, *Spondias purpurea* L.) and species introduced from South America (e.g., *Bixa orellana* L., *Disopyros digyna* Jacq., *Pouteria sapota* (Jacq.) H.E. Moore & Stearn, and *Theobroma cacao* L.) [8]. Plant gathering, honey collection, hunting, and fishing complemented the integrated Mayan production system [9–13].

The use of fire to temporarily displace vegetation and permit cultivation, followed by 16–18 years' fallow to allow the soil to regain fertility were key factors that allowed the *milpa* to adapt to limitations imposed by the northern lowlands' climate and edaphic conditions [14, 15]. With fallow periods exceeding 16 years following cultivation of 2–3 years, the *milpa* system enjoyed a long period of productivity in with permanent rather than nomadic settlement [14, 16, 17].

Colunga-GarcíaMarín and Zizumbo-Villarreal [8] report 32 native plant species used for food and beverages in the Maya lowlands: 17 wild and collected, and 15 domesticated and cultivated. In addition, 30 domesticated species from elsewhere in Mesoamerica and from South America were introduced prior to European contact, bringing the total number of New World food species in the northern Yucatan lowlands to 62 [8]. The generation of considerable intraspecific diversity in *milpa* cultivars was, likewise, a key adaptation to conditions of climate over time and the space [18]. This intraspecific diversity is comprised of morphologically and physiologically distinct varieties with different lifecycle lengths, grain, seed, and fruit colors among maize, bean and squash cultivars, and seed and fruit shapes of bean and squash types.

This richness in maize includes the *Nal tel* race that produces in 2 months and includes variants with different grain colors (e.g., white *sak nal*, yellow *k'an nal*, red *chak nal*, and black *ek nal*). *Xmeje nal* maize produces in 2.5 months with white and yellow variants. *Ts'it bakal* maize is intermediate, producing in 3.5 months, and the long-cycle *Tuxpeño* maize race with white, yellow, red, purple/black, and white/red striped (*pix Cristo—Christ's knee*) produces in 4 months. Among the squashes *Cucurbita moschata* (Duchesne ex Lam.) Duchesne ex Poir., there are short cycle types (*xmejen kuum*) and long cycle types (*xnuk kuum*) with thin-skinned *is* varieties and thick-skinned *tok* varieties. This species' varieties have different shapes (spherical, flattened, pear-shaped) with different colors including green (*chay*), yellow (*k'an*), red (*chak*), and grayish white (*ta'an pose'en*). Among the *P. lunatus* beans (*ib*), we find short cycle (*xmejen*) red and white varieties and long cycle (*xnuk*) varieties of different colors—yellow (*k'an*), red (*chaak sak', chak, chak chí*), black (*box pech*), mottled (*puksikal ts'uts'uy*, *ts'its'iba*, *matsa kitam*)—and shapes—small and round (*mulición*) and flat disks (*uolis*). There are two *P. vulgaris* variants—*xkooli bu'ul* and *tsama bu'ul* [18–19]. *Xkooli* signifies that the product is from the *milpa*.

Establishing the lowland Yucatan Maya food system relied on both cooking techniques and transformation of the ingredients used in the food system used elsewhere in Mesoamerica, including the three-stoned hearth and subterranean ovens lined with stones. Similar cooking technology is found in Europe and Asia as far back as 32,000–30,000 years BP and elsewhere in the New World from 10,500 to 10,000 BP [20–22].

Various studies have established that the lowland Maya diet and consumption patterns have not significantly changed since the first European contact [24–27].

Nevertheless, we lack a structured description of the contemporary Mayan food system in the northern Yucatan area and research on the relative importance of each of the many species and varieties that constitute that system. Nor do we have a clear idea of specific importance of different production methods in the overall food system of the lowland Yucatecan Maya that would allow us to explain its successful establishment and development.

The objectives of this study are first to describe the structure of the food system of the contemporary lowland Maya of the northern Yucatan Peninsula and second to estimate the importance of the different Mayan plant species and varieties of production systems that sustain its inhabitants.

Methodology

Fieldwork took place in the community of Xocén between July 2010 and July 2011, and involved 4 day visits each month. Using participant observation methods among six extended families, we documented the uses, techniques, and other practices related to food preparation and consumption. These families included all of the persons who live in the same compound (*solar*) and who share in food preparation and consumption. A young woman from the community served as a translator.

We inventoried foods and beverages that were prepared and consumed during our monthly visits and included some that were mentioned but not observed. We recorded the time of year they are used and whether they are considered to be daily fare or ritual or ceremonial. Our information lists the dishes' principal ingredients and distinct varieties of the major species used: maize, beans, squash, chilli pepper, and hog plum. The names for food dishes, beverages, and varieties are the vernacular ones used locally.

Study Area. We selected the community of Xocén because it shows many signs of conserving traditional Maya culture as well as being a place where people still grow most of the food that they consume. Xocén is located in the south east of the state of Yucatan at an altitude of 25 masl. Its climate is classified as hot subhumid with summer rains, a dry to semidry winter, annual mean temperature of 25.6 °C and average annual precipitation of 1203.4 mm [28] (Fig. 6.1). The geological substrate is calcareous Karst, and the landscape is a level plain with cambisol soils interspersed with rocky outcrops of a few meters elevation [29]. The vegetation of the area is similar to other parts of northern Yucatan: semideciduous, dry tropical forest.

Xocén has 2039 inhabitants, 99.1 % of whom speak Maya, and is comprised of 393 house compounds with one or more houses and house gardens [30] where fruit trees and spice plants are grown and where fowls are kept and swine penned. Houses are constructed with poles and palm-thatched roofs. Women wear the traditional Mayan *hipil*.

The plant food resources for the local diet are produced in three different agroecosystems—*milpa*, *conuco*, and house garden—as well as through hunting and

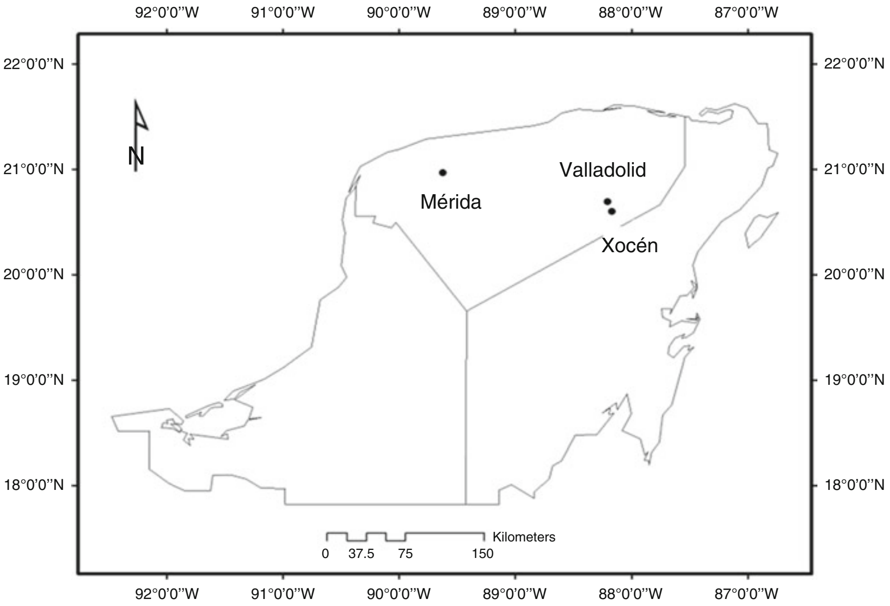

Fig. 6.1 Northern Yucatan Peninsula

gathering. *Milpa* and *conuco* are grown with slash and burn technology in forests with medium growth. Although largely self-sufficient, the people of Xocén also supplement their household production with foods purchased from neighbors selling surplus and in the village's small shops or in the city of Valladolid that is 12 km away.

Results

Foods, beverages, and their ingredients. We registered 74 foods or beverages that were prepared and consumed as daily fare or for ritual or ceremonial occasions during our fieldwork (Table 6.1), plus five others that were mentioned but not prepared. Among foods, we found: 31 main dishes that constitute whole meals, they can be dry or soup-like and are based on meat, eggs, or legumes, and are accompanied by *tortillas*, small discs made of nixtamalized maize dough (*masa*) cooked on a *comal*. Nixtamalization refers to the processing of maize by soaking and cooking kernels in water with lime or wood ash to remove the seed coat [31]; 6 soups or broths that are made with or without meat, vegetables, and legumes and sometimes accompanied by wheat-based pasta; 3 special *tortillas*, two of them prepared by mixing the *tortilla* dough with other ingredients before cooking on the *comal*, and a ceremonial tortilla (*keek*) only for the deities; 8 tamales elaborated with maize dough stuffed with meat, legumes, or *chaya* (*Cnidoscolus chayamansa*), wrapped in leaves, and cooked by

Table 6.1 Foods and beverages registered in Xocén between July 2010 and July 2011, principal plant species and local varieties that are main ingredients, other ingredients and the time of consumption

Foods	Principal species	Other ingredients	Time of consumption
Main dishes			
1. arroz je’	Zm(1or 2)[a]; Cpa(1)[b]	Rice; eggs	All year/daily
2. atún je’		Eggs; canned tuna	All year/daily
3. ba’		gopher; lime	All year/daily
4. beech	Zm(1or 2)[a]; Cpa(2)	Chachalaca; vegetables	December/daily
5. box k’óol	Zm(3)[c] (1or 2)[a]; Cpa(1)	Pork	All year /festive
6. bu’ul	Zm(1 or 2)[a]; Pv(1 or 2)	Mexican tea	All year/daily
7. carnitas	Zm(1 or 2)[a]; Cch[b]	Pork; avocado; sour orange	All year/daily
8. cháachbu’ul	Zm(1 or 2)[a]; Pv (1 or 2); Cch[b]	Mexican tea; onion; lard	All year/daily
9. chay je’	Zm (1 or 2)[a]; Cpa (1 or 3)[b]	Spinach tree; egg	Lent Fridays
10. chirmole jetel bu’ul	Zm(3) (1or 2)[a]; Pv (1 or 2); Cpa(1); Sp (1 or 2 or 3)	Lard	All year/daily
11. chokobil	Zm(1 or 2)[a]	Pork; annato	All year/ceremonial
12. ek	Zm (1 or 2)[a]; Cpa (1)[b]	Wasp larvae; lime	Mar–Apr/daily
13. ekbije’	Zm (1 or 2)[a]; Cpa (1)[b]	Wasp larvae, egg	Mar–Apr/daily
14. iib pideo je’	Zm (1 or 2)[a]; Pl (1); Cch	Pasta; egg	Mar–Apr/daily
15. kaaybije’	Zm (1 or 2)[a]	Egg; tomato; annato	All year/daily
16. k’óolbi je’ abal	Zm (1 or 2)[a] (1 or 2)[c]; Sp (2 or 3 or 4); Cpa (1)[b]	Egg	Mar–Apr/daily
17. k’óolbixperoon	Zm (1 or 2)[a] (1 or 2)[c]; Cm$_{fr,s}$; Cch	Cowpea	Oct–Nov/daily
18. k’óolibu’ul	Zm (1 or 2)[a] (1 or 2)[c]; Pv (2); Cm$_{s}$; Sp (1or 2 or 3); Cpa(1)	Chives; tomato	All year/daily
19. k’ek’en bu’ul	Zm (1 or 2)[a]; Pv (2); Cch[b]	Pork; onion; lime	All year/daily
20. mukbikaax	Zm (1 or 2)[a]; Cpa (1)[b]	Chicken	All year/daily
21. panuchos	Zm (1 or 2)[c]; Pv(1 or 2); Cch[b]	Chicken; tomato; onion	All year/daily
22. pibikek’en	Zm (1 or 2)[a]; Cch[b]	Pork; annato; sour orange	All year/festive

(continued)

Table 6.1 (continued)

Foods	Principal species	Other ingredients	Time of consumption
23. pibilceh	Zm (1 or 2)^{a}; Cch^{b}	Venison; onion; tomato	All year/daily
24. pipirión xréenteja	Zm (1 or 2)^{a}; Cm$_{s}$;Sp (1or 5)	Pigeon pea	Apr–Sep/daily
25. toksel	Zm (1 or 2)^{a}; Pl (1 or 2 or 3); Cm$_{s}$; Cch^{b}	Chives; coriander	All year/daily
26. tsaajbi ajos jetel sakan	Zm (1 or 2)^{a}(1 or 2)^{c}; Cpa (4)^{b}	Chives; lard	All year/daily
27. tsaajbi kuum	Zm (1 or 2)^{a}; Cm$_{fr}$; Cpa (4)^{b}	Lard	Sep–Oct/daily
28. tsub	Zm (1 or 2)^{a}; Cpa (1)^{b}	Agouti	when is available
29. xperoón	Zm (1 or 2)^{a}; Cm$_{fr}$; Cch^{b}	Cowpea; pork fried skin	Oct–Nov/daily
30. xréenteja jetel k'ek'en	Zm (1 or 2)^{a}; Cpa (5)	Pigeon pea; pork; onion; sour orange	Apr–Sep/daily
31. xt'so pak'	Zm (1 or 2)^{a}; Cm$_{s}$; Cch^{b}	Tomato; coriander; chives	All year/daily
Soups			
32. caldillo je'	Zm (1 or 2)^{a}; Cpa^{b}	Egg; spinach tree; pasta	All year/daily
33. chakbilchay	Zm (1 or 2)^{a}; Cm$_{s}$; Cch^{b}	Spinach tree; lime	Lent fridays
34. chakbilkaax	Zm (1 or 2)^{a}; Cch^{b}	Chicken;vegetables	All year/daily
35. chochpideos	Zm (1 or 2)^{a}; Cch^{b}	Blood pork susage; pasta; annato	All year/daily
36. joroches	Zm (1 or 2)^{c}; Cm$_{fr}$; Cch^{b}	Lime	Sep–Oct/daily
37. xréenteja jetel sopa	Zm (1 or 2)^{a}; Cch^{b}	Pigeon pea; pasta	Apr–Sep/daily
Special tortillas			
38. axi tzerek	Zm(1,2)^{c}; Cm$_{s}$		All year/daily
39. is waaj	Zm(1,2)^{c}	Sugar; lard	Oct–Nov/daily
40. keex	Zm(1 or 2)^{c}		All year/ceremonial
Tamales			
41. chachakwaaj	Zm (1 or 2)^{c}	Annato; pork or chicken; tomato	All souls' day /festive
42. chayiwaaj	Zm (1 or 2)^{c}; Cpa (1)^{b}	Spinach tree; lard	All year/daily
43. chochiwaaj	Zm (1 or 2)^{c}; Cch^{b}	Chicken guts; onion; sour orange; coriander	All year/daily
44. makulaniwaaj	Zm (1 or 2)^{c}; Pl (2); Cm$_{s}$; Cpa (1)	Mexican pepperleaf; chives	Jan–Feb/daily
45. xkooy ts'u	Zm (1 or 2)^{c}; Pl (2); Cm$_{s}$; Cpa (1)	Chives	Jan–Feb/daily

(continued)

Table 6.1 (continued)

Foods	Principal species	Other ingredients	Time of consumption
46. pich'ich'	Zm (1,2)[c]; Cpa (1)[b]	Cowpea; lard	Ago–Nov/daily
47. tamalí	Zm (1 or 2)[c]; Cpa (1)[b]	Chicken; lard; tomato; onion	Christmas/festive
48. vaporcitos	Zm (1 or 2)[c]; Cpa (1)[b]	Chicken; cowpea; lard	November/daily
Vegetables			
50. chakbilnal	Zm (all varieties)		Oct–Nov/daily
51. chakbilxka	Zm (1 or 2)[a]; Cch[b], Ca_{fr}	Lime	September/daily
52. mukbilcebolla	Zm (1 or 2)[a]	Shallots; lime	Nov–May/daily
53. pibilnal	Zm (all varieties)		October/ceremonial
54. xka lol	Zm (1 or 2)[a]; Ca_{fw}; Cpa (1)[b]	Lime	September/daily
Others			
55. kutbipak	Zm(1or 2)[a]; Ca_s; Cch[b]	Tomato	All year/daily
56. pibikuum	Cm_{fr} (2 or 3 or 4)	Sugar[b]	November/daily
57. putsika'gracia	Zm(1or 2)	Honey bee	All year/ceremonial
58. sak iis, kan iis		White and yellow sweet potatoes	Nov–Mar/daily
59. sak tsiín		Manioc; honey bee	Nov–Apr/daily
60. sikilkab	Cm_s	Honey bee	All year/daily
61. sikilpak	Zm(1 or 2)[a]; Cm_s	Tomato; coriander	All year/daily
62. sikliabal	Zm(1or 2)[a]; Cm_s; Sp (2 or 5)		Apr–Sep/daily
Beverages			
Atoles		Cacao; sugar; sweet crackers	All year /daily
63. chakbiixim	Zm(1 or 2)[c]	Milk; cinnamon	All year/daily
64. checheixiim	Zm(1or 2)	Sugar	Mar–Oct/daily
65. chokosakan	Zm(1 or 2)[c]		All year/daily
66. chujuk paj sa'	Zm(1 or 2)[c]	Sugar	Oct–Nov/daily
67. chujuk sa'	Zm(1 or 2)[c]	Sugar	Oct–Nov/daily
68. paj sa'	Zm(1 or 2)[c]; Cpa(1)[b]	Salt[b]	Oct–Nov/daily
69. sa'	Zm(1 or 2)[c]; Cpa(1)[b]; Cm_s[b]	Salt[b]	Oct–Nov/daily
70. saka'	Zm(1or 2); Cm_s[b]		All year /ceremonial
Others			
71. tablilla		Cacao; sugar; sweet crackers	All year /daily

(continued)

Table 6.1 (continued)

Foods	Principal species	Other ingredients	Time of consumption
72. xton leky	Zm(4); $\mathrm{Cm}_{\mathrm{fr}}(2)$	Sugar	Good Friday
73. coco keyem	Zm(1 or 2)^{c}	Coconut; sugar	Lent
74. ta'an u'kul	Zm(3)	Cacao; sugar; species	All year/ceremonial

Species: Zm *Zea mays,* Pv *Phaseolus vulgaris,* Pl *Phaseolus lunatus*, Ca *Cucurbita argyrosperma*, Cm *Cucurbita moschata*, Cpa *Capsicum annum*, Cch *Capsicum chinense*, Sp *Spondias purpurea*
Varieties: *Zea mays* (1, sak nal; 2, k'an nal; 3, ek chob; 4, xtilib xchun ya); *Phaseolus vulgaris* (1, tsama'; 2, kooli bu'ul); *Phaseolus lunatus* (1,sak ib; 2 chaak sak'; 3 mulición); *Cucurbita moschata* (1, iis k'uum; 2, xtoobox; 3 wolis k'uum); *Capsicum annum* (1, chawa ik; 2, chuju'uk ik; 3, sukurre; 4, pica paloma; 5, xkat); *Spondias purpurea* (1, batunil; 2, tuspana; 3, campech; 4, xowen; 5, tuxiló)
Form of use: ^{a}tortillas; ^{b}optional; ^{c}masa (from maize soaked with lime) as an ingredient
Part used from Cucurbita spp.: ($_{\mathrm{fr}}$, fruit; $_{\mathrm{fw}}$, flower; $_{\mathrm{s}}$, seeds)

steaming or by immersion in chicken broth; 6 dishes made with fresh vegetables that have been boiled or baked (fresh maize, squash flowers or fruits, *chaya*, and onions); and eight others that are sweet foods that incorporate squash fruit or seed, or sweet potatoes or manioc that has been boiled or baked, they also are fresh sauces with tomato, squash seed, and hog plum that are eaten with tortillas.

Among the beverages listed in our inventory are eight types of *atole*, the Mesoamerican maize-based drink. These range from sweet to salty, acidic (as a result of a light fermentation) or non-acidic. In addition, we found four sweet beverages that are mostly consumed cold, with or without maize or cacao.

Ceremonial dishes and drinks are prepared as offerings to local deities, ancestors, or supernatural beings to solicit favors or as thanks for favors granted. After the ceremony, these foods and beverages are consumed and drunk by the participants. An exception is the *keek* dish made with miniature tortillas (1.5 cm of diameter) and exclusively dedicated to supernatural beings.

The five daily fare dishes mentioned but not prepared during our fieldwork were: *ta'chak*, made with maize fungi (*Ustilago maydis* (DC) Corda); *xuux*, made with wasp (*Polybia* sp.) larvae; *xnook'ol*, made with the fall armyworm (*Spodoptera frugiperda* Walker) that attacks green maize; *wolbiskil*, soup made with balls of ground squash seed; and a coconut (*Cocos nucifera* L.) sweet. The last two were not prepared because of the belief that the presence of visitors would spoil them, and the rest due to the lack of ingredients.

Various dishes combine the principal species of the *milpa* (maize, beans, and squash) with chili pepper. Others add produce from the house garden, hog plum, and *chaya* leaves. Numerous dishes and beverages combine maize and squash fruit or flowers flavored with chilli pepper. Species from the *conuco* system, makal (*Xanthosoma sagittifolium*), manioc (*Manihot esculenta*), and sweet potato (*Ipomoea batatas*), are boiled or baked and eaten only at a minor scale.

Figure 6.2 presents the combinations of species used in food dishes and how these foods are cooked. This figure excludes introduced species, such as *Vigna unguiculata* (L.) Walp. and *Cajanus cajan* L. Huth., that are only occasionally used as substitutes for beans.

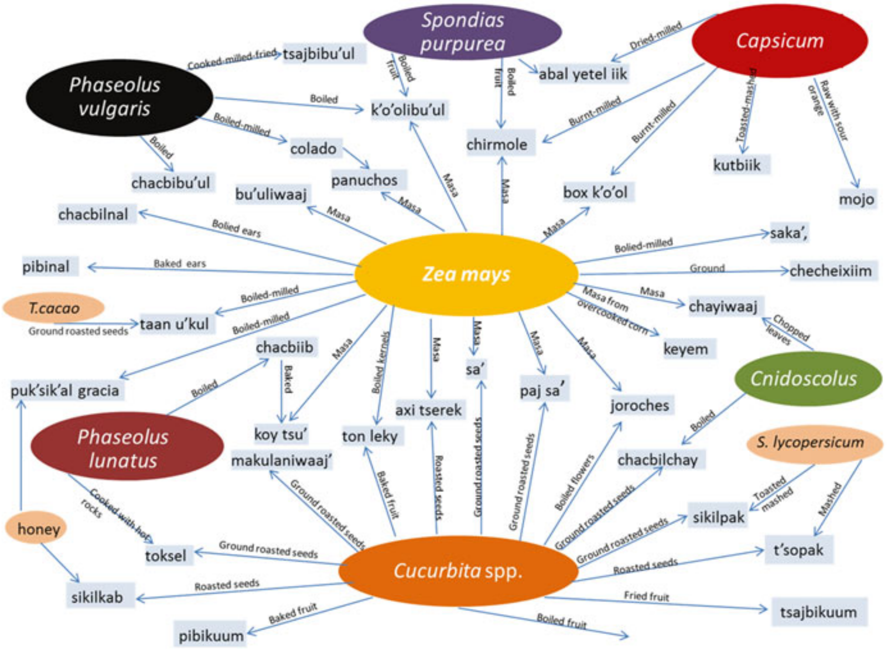

Fig. 6.2 Combinations of the native plant species used in the contemporary Mayan cuisine and cooking techniques

Relative Importance of Plant Species

Among the 74 foods and beverages registered in Xocén, 91.9 % include maize, 29.7 % include squash, 12.1 % beans, 12.5 % chilli pepper, 6.7 % hog plum, and 5.4 % *chaya* (Table 6.2). Since foods and beverages may contain more than one species, the total percentage in this list exceeds 100. Maize is included whether as an ingredient or in tortillas that are part of the food dishes. Maize is neither substitutable nor dispensable; and other species, such as chilli pepper, are only counted when actually used rather than optional.

Maize is the principal ingredient of 28 foods and beverages—37.8 % of the total—and is an accompaniment in 40 others as tortillas. Only four dishes do not use maize: manioc in honey, sweet potato in honey, squash (*C. moschata*) baked in earth ovens, and *sikilkab*—squash seeds sweetened with honey.

Squashes are used in 22 foods and beverages (29.7 %), with their seeds most commonly employed (13 of them). The seeds of mature *C. moschata* are eaten without hulls and generally ground; while fruit of both young and mature *C. moschata* plants is eaten. The fruit of very young *C. argyrosperma* is eaten, while seeds from mature plants are toasted whole and eaten in both daily and ceremonial meals, such as the ceremony to mark the entrance of newborns into social life (*hetzmek*). The flowers of both of these squash species are used in two dishes: *lol xka* and *joroches*.

Table 6.2 Relative importance of the food plant species registered in Xocén between July 2010 and July 2011 (from a total of 74 foods and beverages)

Species	Varieties	N° of food or drinks as primary or essential ingredient	N° food or drinks as optional ingredient or accompaniment	Overall % of food and drinks
Zea mays	*ek chob*	28	40	91.9
	k'an nal			
	sak nal			
	xtilib chun ya			
Capsicum annuum	*chawa ik*	7	15	29.7
	chuju'uk ik			
	picapaloma			
	sukurre			
	xkat			
Capsicum chinense	*habanero*	2	17	25.6
Cucurbita moschata	*is k'uum*	17	2	25.6
	wolis k'uum			
	xtoobox			
Phaseolus vulgaris	*tsamá bu'ul*	5		6.7
	xkooli bu'ul			
Spondias purpurea	*batunil*	5		6.7
	campech			
	tuspana			
	tuxiló			
	xowen			
Phaseolus lunatus	*chaak sak'*	4		5.4
	mulición			
	sak ib			
Cnidoscolus chayamansa	*chay*	4		5.4
Cucurbita argyrosperma	*xka*	3		4

Beans are components in ten food dishes (12.1 %). The commonly used are two black bean varieties of *P. vulgaris*, *tsama' bu'ul* and *kooli bu'ul*, that are ingredients in six different dishes that are part of daily fare. In contrast, *P. lunatus* is only eaten occasionally (4 dishes) and primarily immediately after the harvest of young or mature beans. This species is used in two types of tamales—*xkoy tsu* and *makulaniwaaj*—and *toksel*, a dish whose cooking is finished on by placing hot stones in the cooking pot. All of these dishes employ three varieties of *P. lunatus*: *sak*, *mulición* y *chaak sak*'.

Chilli peppers are important components and are obligatory in 7 dishes (12 %) and optional accompaniment in 32 others. Seven varieties of *Capsicum annuum* were registered—*chawa, chu'ujuk, kuum, maax, pica paloma, sukurre and xkat*—while *C. chinense* Jacq. only registered two varieties—*yax* and *k'an*. In Xocén, dishes that include the *yax* variety of *C. chinense*. require that it be red at maturity, recorded by us as *habanero*. While the *chawa* variety grows in *milpas*, all of the other chili pepper varieties are grown in house gardens, allowing the women to tend them carefully and to use them in almost all cooking.

We registered five dishes (6.7 %) cooked with different varieties of immature hog plum: *butunil, campech, tuspana, tuxiló, xowen.* This fruit from house gardens is also eaten fresh when mature and can be harvested in different seasons. *Chaya* is an important element in four plates (5.4 %) and is eaten year round, although it is most abundant during the rainy season. We did not find varietal differences in edible *chaya*.

Variety selection in foods and beverages preparation. The most common foods and beverages using maize as a primary or essential ingredient are tortillas, tamales, and *atoles*, and for these, white (*sak*) or yellow (*k'an*) maize, from either short- or long-cycle races, is used. Short-cycle maize is used as a back-up to the long-cycle types: it is available before the main harvest and when stocks of the previous harvest are depleted. The first green ears of short-cycle maize are cooked in earth ovens (*pibinal*) and looked on as an offering along with other foods and beverages made with new, fresh maize—*atole* (*sa'*), boiled ears of maize (*chakbilnal*), and toasted tortillas made from new maize (*iswaaj*).

For festival foods and beverages related with various ceremonies, there is a preference for black or red varieties. The most common festival food is *boox k'óol*, a pork dish made with purple maize (*ek chob*) that is combined with the *chawa* chilli pepper variety that has been burned to yield a black sauce. The ceremonial beverage *ta'an u'kul* is prepared from black or purple maize mixed with toasted cacao. The Lenten dish *xton leky* is made with whole maize kernels for the reddish *chun* variety mixed with squash pulp.

Fruits and flowers of short-cycle types of *C. moschata* and *C. argyrosperma* with delicate skins are used to prepare *joroche* soups. Long-cycle and thick-skinned types of these species are used for their seed, and *C. moschata*, especially the *axi* variety with a warty skin, is baked in underground ovens. All forms of these squashes are used except the pear-shaped *kalim* variety which is fed to animals kept in the house garden.

The most commonly used *Capsicum annuum* variety is *chawa* that is dried and then toasted, baked or fried before grinding. Sweeter and milder varieties *ch'ujuk* and *xkat* are added whole or in large pieces to stews during cooking. *Sukurre* and *picapaloma* are occasionally eaten after roasting and grinding. *Maax* and *kuum* chilies are seldom eaten. *Capsicum chinese* is used uncooked and often mixed with red onion, cilantro (*Coriandrum sativum* L.), and sour orange (*Citrus* × *aurantium* L.) to make a garnish called *mojo*. This capsicum is only used as an ingredient in one dish, *ib pideo jé*, a soup made with *P. lunatus*, wheat noodles, and eggs.

The most preferred hog *plum* variety in Xocén cooking is *xowen*, while the fruits of the *tuxiló* and *tuspana* varieties are preferred as fresh plums. Selection depends on the season when a particular hog plum variety is available, although the major harvest for this fruit is between March and May, coinciding with the season of Lent in the religious calendar when meatless dishes are eaten.

Discussion

Foods, beverages, and their ingredients. The majority of foods and beverages incorporate three species that have been the base of the Mesoamerican food system since Pre-Columbian times—maize, beans, and squash—and which are complementary to each other ecologically, agronomically, and nutritionally [3]. Maize provides the bulk of carbohydrates and some protein [32, 33]. *P. vulgaris* and *P. lunatus* beans provide proteins [34] as does *chaya* [35]. Squash seed deliver fatty acids and protein [36] and *chaya* leaves and fruit from squash, chili, hog plum offer vitamins and minerals [37].

Many of the foods and beverages in our Xocén inventory are possibly of pre-European origin [38] that have been preserved as part of Maya traditional food ways or "food culture" that has given a balanced diet to the people of Xocén and elsewhere in Yucatan. Zizumbo-Villarreal et al. [4] suggest that the diet of western Mesoamerica in the Archaic Period was assembled for the wild ancestors of domesticated plants and that their nutritional complementarity might have given incentive for domestication and the development of the *milpa* agro-ecological system. This system also attained agro-ecological complementarity.

We found many foods in Xocén that were also registered by Cázares-Sánchez and Duch-Gary in another Mayan community, Yaxcabá, in Yucatan [27]. There, maize, squash, beans, and chilli were also the principal ingredients among the 60 foods and beverages mentioned by the researchers. Among these, maize was the principal ingredient in 20. This proportion is slightly smaller than what we found in Xocén (28 dishes out of 73).

Relative importance of plant species and production systems. Maize, squash, beans, and chilies are the species at the nucleus of the Maya food system in Xocén, and all are produced in the *milpa*. Most *Capsicum* and all *Spondias* and *Cnidoscolus* come from house gardens. The *conuco* system is responsible for manioc, *makal*, and sweet potato that are present but relatively unimportant in Xocén's food system. Plant gathering, gathering insects and honey, and hunting are incidental and less important than in other areas of Mesoamerica.

Food dishes using ingredients introduced from outside of Mesoamerica, such as wheat-based pasta, chicken eggs, chicken, pork, and lard are common but usually mixed with local, Mesoamerican ingredients. Non-Mesoamerican staples, such as rice or lentils, and processed foods, such as canned tuna or sardines, are rarely consumed in Xocén.

Variety selection connected to foods and beverages. We found that white and yellow maize varieties were used for making the normal, daily tortillas and tamales.

White maize is preferred and this preference is attributed to the softness and ease of working with its *masa* characteristics, also mentioned by Cázares-Sánchez and Duch-Gary [27]. Nevertheless, the use of mechanical mills to grind maize into *masa* obscures these qualities of white maize varieties. Our informants told us that *masa* is made with the maize that is on hand, regardless of variety. A similar finding is reported by Perales et al. [39], who noted the absence of strong preference for different maize varieties for making tortillas in different parts of Mexico.

Foods and beverages using black, purple, or red maize have ceremonial importance. This suggests that preference for maize variety based on color does exist, but perhaps not for daily use in staples such as tortillas and tamales. Aguirre Gómez et al. [40] likewise found this preference for maize color in the preparation of special foods in Guanajuato. These findings echo those of Hernández X. [41] about the preparation of blue tortillas for festival days and the use of certain maize varieties for the beverages *pinole* and *atole,* and for *totopos*—a type of tortilla baked in clay ovens that is prepared in the Oaxaca portion of the Isthmus of Tehuantepec.

Within the Mayan world-view, the basic color of distinct maize varieties relates to the four cardinal points of Earth and sky: white (*sak*) represents north (*xaman*), yellow (*k'an*) connects to the south (*nohol)*, red (*chak*) corresponds to the east (*lak'in*), and black (*ek*) relates to the west (*chik'in*) [42]. These four cardinal directions are also associated with the four gods (*Cantul Ti Ku*) mentioned in the creation myth found in the Chilam Balam of Chumayel [43]. The intersection of these four directions defines the axes of both the Earth and Universe in the cosmologies of the Maya and groups throughout Mesoamerica [44]. From a nutritional standpoint, blue and purple maize is reported to have high levels of anthocaynins that have antioxidant properties and thus may serve as anticarcinogens [45]. Apart from buttressing local cultural aspects, conserving these colored maize varieties may have an additional health benefit.

In contrast to other places in Mesoamerica where squash consumption has declined [46], these species, especially their seeds continue to be important dietary components in Xocén. The bulk of the harvest of both species (*C. moschata* and *C. argyrosperma*) is dedicated to obtaining seed that is conserved in jars for use throughout the year to provide a distinct flavor to regional cooking in sweet and salty foods as an accompaniment in diverse dishes and beverages. In *C. moschata*, the type of skin is a key characteristic for the cooking method. Thick-skinned varieties, such as *xtoop* and *axi*, are preferred for earth-oven concoctions. In contrast, the variety has a thin skin unsuitable for baking in earth ovens. Thus, we can see that the preservation of different varieties, with distinct culinary properties, depends in large part on the way they are cooked. The sweetness of the squash pulp from young and mature plants is prized for salty dishes.

In contrast to the 12 varieties of *P. lunatus* reported in Xocén in previous studies by Martínez Castillo [47] and Terán et al. [26], we found only three varieties of in use in 2010–2011. This suggests a rapid loss of varietal richness in this species that may be caused by adverse environmental conditions such as drought or cyclones mentioned by informants or changing consumption patterns. Reasons for this loss also include that children consider some *P. lunatus* varieties to be disagreeable, their long cooking time, their high cost if not grown at home, and a preference for white varieties because of their similarity to butter. Moreover, a belief exists that if these beans are cooked over certain types of firewood, they will have a bitter flavor in subsequent harvests. Consequently, people avoid selling, giving, or exchanging *P. lunatus* because they cannot be sure if they will be cooked with the proper firewood. This provides an example of how cultural attitudes may affect the conservation of certain varieties.

Besides these cultural factors that have reduced diversity in *P. lunatus* in Xocén, exotic species such as cowpea, *Vigna unguiculata*, and pigeon pea, *Cajanus cajan*, have displaced *P. lunatus* in food dishes such as stews, *pipianes* (dishes with sauces using squash seed), tamales, and *toksel* prepared with beans and squash seeds that have been toasted and ground. These introduced species are grown in the house garden and can produce up to two harvests per year. Nevertheless, the primary reason for the displacement of *P. lunatus* appears to be changed in local taste preferences. In contrast, common beans (*P. vulgaris*) continue to be an important component of ordinary meals and are purchased if local production is insufficient, as during the year of our fieldwork period.

Regardless of availability, chillies are used differently depending on pungency, flavor, and how they complement main dishes. This differential use and preference for using local chillies that are stewed, as well as uncooked *habanero* (*C. chinese*), was observed also by Latournier et al. [48] and Cázares Sánchez et al. [49]. Cázares Sánchez et al. [49] registered seven morphotypes of *C. annuum* along with a close relation between capsaicinoid content and specific culinary use, suggesting specific use has contributed to both diversification and conservation. Genetic studies point to the Yucatan Peninsula as a possible center of domestication and diversification of *C. annuum* [50].

The high diversity during the year of varieties of *Spondias purpurea* is particularly interesting. Ten varieties of this fruit have been described in Yucatan [51], and we find eigth varieties in Xocén, where they continue to be an important ingredient in food dishes by contributing a distinct regional and acidic flavor. Here, as throughout almost all of Mexico, people have a notable preference for acidic flavors. This may help explain the widespread use of exotic fruits in Yucatan's kitchens, such as sour lemons (*limón)*, sour oranges, and sweet lemons (*lima*). Consuming diverse types of the hog plum owes to their availability at different times of year, although the major harvest occurs in March and April. The preference for their taste characteristics in each dish is not as clear or distinctive as for chillies. Other plants that provide acidic flavors are the red tomato (*pak* and *tsu'um pak,)* produced in the *milpa* and sour nance or *sak paj* (*Byrsonima bucidaefolia* Standl.) grown in house gardens. The former maintains its acidity in contrast to commercial varieties.

Finally, introduced condiments such as oregano (*Lippia graveolens* Kunth), and others from the New World, such as the Tabasco pepper (*Pimenta dioica* L. Merr.) and *achiote* (*Bixa orellana*) are essential elements in Mayan cuisine in Yucatan. A mixture of garlic (*Allium sativum* L.), onion (*Allium cepa* L.), allspice (*Pimenta dioica*), and oregano, all exotic to Yucatan, is called *xaak* and is added to virtually all food dishes. *Xaak* may help ward off infectious disease because of the antimicrobial properties that are reported for its four species. The antibacterial activity of allspice is reportedly triggered by the addition of the citrus (*Citrus × aurantifolia* (Christm.) Swingle) [52] that is commonly used in Mayan cooking along with (*Citrus aurantiaca* (L.) Swingle). The introduction of condiments such as *Allium*, black pepper (*Piper nigrum* L.), coriander (*Coriandrum sativum*) along with the citrus mentioned above have not displaced native Mayan seasonings but rather have been incorporated into the existing suite of condiments.

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Chapter 7
Traditional Markets in Mesoamerica: A Mosaic of History and Traditions

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Abstract This contribution discusses the different types of markets, *tianguis* (traditional producer markets) and trade relations which have occurred in Mexico in different historical periods. The comparison of such major pre-Hispanic cultures as the Aztecs, Mayas, and Purépecha highlight the role of the long-distance traders or *pochteca*. During the Viceroyalty Period, *alcabalas* (taxes) registered in the documents reveal the continuity of the trade routes based on pre-Hispanic roads and exchange of products from different ecological zones. For Independent Mexico Period, the commercial circuits that supplied urban areas are characterized by those of Puebla. This analysis suggests that the marketing in contemporary Mexico is a consequence of the relationships established during the different historical periods. These relationships are reflected in the *tianguis* and contemporary markets as well as products today. The exchange and marketing chains have been influenced and driven by transportation systems, such as the train network at the time of the Porfiriato Period, and currently by the highway systems and mechanized transport vehicles. As a result, today's exchange system is characterized by a larger scale, a greater distance and the phenomenon of the central markets while *tianguis* are located in peripheral circuits. The botanical products that are sold and exchanged in the commercial circuits reflect the cultural exchange, based on traditional knowledge, and the exploitation of the natural resources from different ecological zones. Contemporary Mexican studies illustrate the influence of the central market on the demand of plants with novel applications and draw attention to the danger of the overcollection of wild species due to the effect of the emerging demands, hence defending the need for conservation of natural habitats.

Keywords Traditional markets • Tianguis • Trade • Mesoamerica

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Introduction

In order to study the markets, marketing and their influence on the management of biotic resources in Mexico today, one needs to visit the past so as to understand the roots of plant–human relationships. In this contribution we analyze various factors associated with contemporary marketing of plants and their products. They are results of multiple interactions, selection of useful plants, introduction of species and changing values over time in order to meet cultural needs.

Since pre-Hispanic times, diverse and intricate supply chains, tributes, and distance trading were constructed by such dominant cultures as the Aztec, Maya and Purépecha so as to provide access to natural resources in different ecological zones. Their communication network and conveyance via human carriers (*tameme*) and traders (*pochteca*) facilitate the interchange of resources and products among major urban centers of Tenochtitlan, those in the Maya domain, and the Purépechan capital, Tintzuntzan. After the Spanish conquest, the Viceroyalty appropriated these routes that became the main roads for moving products into the central highlands; later, many were transformed into railways and highways upon which we circulate today. These routes favored the exchange of products between tropical lowlands and temperate highlands and converted into the groundwork for contemporary exchange networks. The occurrence of these products in today's *tianguis* (local markets) depends upon various factors including the seasonality, the commercial value, the social significance, as well as the community calendars related to religious and civil feasts. Hence, the variety of products, including those derived from plants, is a consequence of the intricate relationships, culturally based decisions, and social actions.

In this paper we analyze some factors and relations as a thread between historical periods so as to illustrate the selected forms and traditions of marketing of products that have enabled Mexican markets to showcase the relationships between plants and humans. The sources of information presented vary among the different historical periods. The pre-Hispanic era relies primarily on archaeological studies and first observations recorded by the conquerors who visited the tianguis. During the Viceroyalty epoch, taxes on select products and importation provide a perspective on certain vegetal products. Taxation data from the Independent Mexico period continue supplying information as well as products distributed by the railroad system. The contemporary period focuses on additional aspects such as continuity and the effect of the central market on product demand. As a consequence, recent studies deal with the harvesting pressure on the plants, the continuity of trade routes as well as the diversity and the management of certain useful plants.

The Market and the Tianguis

The word market comes from the Latin word "mercatus" which means a designated public place where goods or services are sold, bought or exchanged permanently or on certain days [1]. Meanwhile the word *tianguis* comes from the Nahuatl term *tianquiztli* which denotes "the day when producers gather in order to sell or exchange their products" [2] at a specific place; currently terms "square" or *plaza* can be applied and will used interchangeably with *tianguis*.

Traditionally the *tianguis* is not permanent but occurs on specific days of each week. Market refers to a permanent public place, where the products are available every day of the week. The market place also functions as meeting site for cultural exchange and social encounters. Since pre-Hispanic times in Mexico, markets have played an active role in the social and economic lives of the people who used these locates [3].

Economic interactions take place in markets as they are places where many people meet for different purposes such as buying and selling of products, bartering (or exchange of goods in kind), investigating local production, and surveying product preferences, among others [4]. A local market is the natural point of accumulation of goods, serves as a mobile warehouse, attracting other buyers from larger networks, and is a fixed point of exchange of resources between political and social segments of the economy. Usually in these scheduled temporary markets or *plazas*, the traditional flow of goods is managed by the producers themselves. Economic plans and decisions to participate in the tianguis originate in the family [5].

Members of the market community include among others buyers, sellers, collectors, producers, and *regatones* (resellers). Marketing creates revenues that complement incomes that families generate from agricultural products. In addition to local products, those derived from regional and introduced sources are marketed.

The gender difference of vendors is important. Several studies have documented that women mainly perform marketing activities and barter in the *tianguis* [6–8]. In the case of *tianguis* of Ozumba, State of Mexico, older women usually offer and sell plants while being accompanied by their daughters and daughters-in-law. The sons and husbands may be present but remain in the background without being involved in the sale. A similar pattern is recorded for Comalcalco, Tabasco [9].

In the words of Hernandez Xolocotzi [2], a number of phenomena in the *tianguis* can be studied such as:

> … A) the ecological environment, b) the culture of the people of the area under study, c) the characteristics of wild, domesticated or semidomesticated plants used and d) the socioeconomic environment, in part. Here you can visit to learn: a) the materials produced in the region, and b) the materials brought from other regions. It is also a source of information about: a) forms of production, and b) the degree of domestication of the species. One can obtain seeds or propagules of poorly known useful plants.

Pre-Hispanic Time

In pre-Hispanic times, goods of different classes of society were accumulated and exchanged for alternative products in the market. In Aztec *tianguis* the networks of the state's tribute system converged with the surplus of the elite class, the foreign goods purchased in distant lands. Hence, it was the economic center of the Aztec Empire. In other regions, such as that of the Purépecha, their conquests provided access to resources of the "hot land" where, with irrigation, two crops of tomatoes, chilli peppers, cotton, and various fruits were produced annually and made available to the inhabitants of the cooler highlands [10] through the *tianguis*.

Descriptions of the Tianguis

When the Spaniards visited the *tianguis* of Tlatelolco, Hernán Cortés in his Second Letter of Relationship [11] reported that in this city (Tenochtitlan) existed:

> A market where almost daily over thirty thousand souls, sell and buy… In this market there many things for sustenance as well as for clothing and footwear, they can try and do sell… a lot of firewood and charcoal, and edible and medicinal herbs.

Sahagún [12] for his part gave a more detailed description of the products sold in the same *tianguis* of Tlatelolco, and highlights the great order that existed:

> … and were well cared for by gentlemen so as to avoid frauds in the *tianguis*. They maintained order, selling gold and silver, precious stones, rich feathers of all kinds… elsewhere were those selling cocoa and aromatic spices… elsewhere were those selling blankets, foods such as white maize, black, red and yellow and black beans as large beans and amaranth seed of such colors as ashy brown and red and yellow and white chia, black, and another called *chiantzotzol* … also salt and animals, honey from bees and *maguey*, a great variety of chilies such as tonalchili, chiltepin; tomatoes called miltomates … Elsewhere orderly stands sold fruits, potatoes and root vegetables, *chayote*, squash, squash seeds, herbs, and small onions. Also sold are paper, white incense and black rubber called *ulli* and lime and knives and firewood and wood house construction as well as boards. There were also those who sell cigars as well as many more products.

The pre-Hispanic markets were well supplied as seen from these descriptions. The Spaniards admired these distribution systems that were clean, organized, well-ordered, and harmonious. As a consequence, the Aztec market system was the first native institution that they introduced throughout their colonies so as to maintain their countrymen well supplied. They so jealously appropriated the *tianguis* phenomena that they tried to restrict its operation in Indian villages in order to redirect the supplies to the Spanish cities [13].

Distance Trade in Mesoamerica

Mesoamerica includes an area of what is now part of Mexico, Belize and Guatemala, along with Honduras and El Salvador. Civilizations that flourished within this territorial unit share many cultural characteristics. Within Mesoamerica, five cultural areas were recognized based upon their peculiarities: Central Highlands, Gulf Coast, West Mexico, Oaxaca area, and Maya area [14].

An extensive network of routes integrated Mesoamerica with the primary purpose of facilitating exchange of various commodities. The study of these ancient roads is critical to archaeological research in order to understand social development and reconstruct multiple aspects of cultural interactions [15]. In addition, contemporary marketing and the location of trading centers (e.g., markets, *tianguis*, and *plazas*) are based upon prehistoric linkages as are the many products that have maintained their cultural and economic importance.

The complex and extensive transportation routes were essential for the procurement of goods characteristic of various ecological regions. The products obtained by the distance commerce and a portion of the tribute surplus were concentrated in the *plaza* or *tianguis*. In addition, there was another type of long-distance trade that was under the control of *pochteca* in Nahuatl, *muyul* in Huastec, and *ppolom* in Maya [14].

Central Highland Pochteca

The *pochteca* initially came from the settlement named Pochtlan. Later the term was applied generically to Mesoamerican long-distance merchants (who laid the foundations for the trade routes). There were several categories, varying from rich *pochteca* with headquarters in large cities to those not well capitalized and who moved from one market to another. The poorer local merchants traded salt, pepper and vegetables that they produced themselves [14].

The rich *pochteca* specialized in expensive, select manufactured objects that were light to carry in order to benefit economically from the costly long routes. At that time, cargo was carried by porters (*tameme*) hired for such purpose. They returned with valuable raw materials that were essential craftsmen of Tenochtitlan and financed the cost of such long-distance trade. Some items exchanged in the Central Highlands included [16]:

> … Garments richly designed, skins of rabbit fur, green obsidian, ornaments of gold and precious stones. In exchange, they brought cacao, cotton blankets, salt, shells and snails, feathers from quetzal and other birds, jaguar skins, jade, amber, dyes, rock crystal and copal.

The *pochteca* had great mobility and travelled mainly along two routes. Some marched to the south while others to the east and southeast of Mesoamerica. They departed from Tlatelolco/Tenochtitlan, Texcoco, Cuautitlan, Atzcapozalco, Culhuacán, Chalco, Amecameca, Cholula, and Tepeaca heading to localities in the present-day states of Puebla, Guerrero, Oaxaca, and Veracruz [17] (Fig. 7.1).

Maya Area

The Maya maintained commercial circuits around the Yucatan Peninsula in order to promote internal exchange. At critical points sanctuary markets were established to ensure rapid circulation of products [16]:

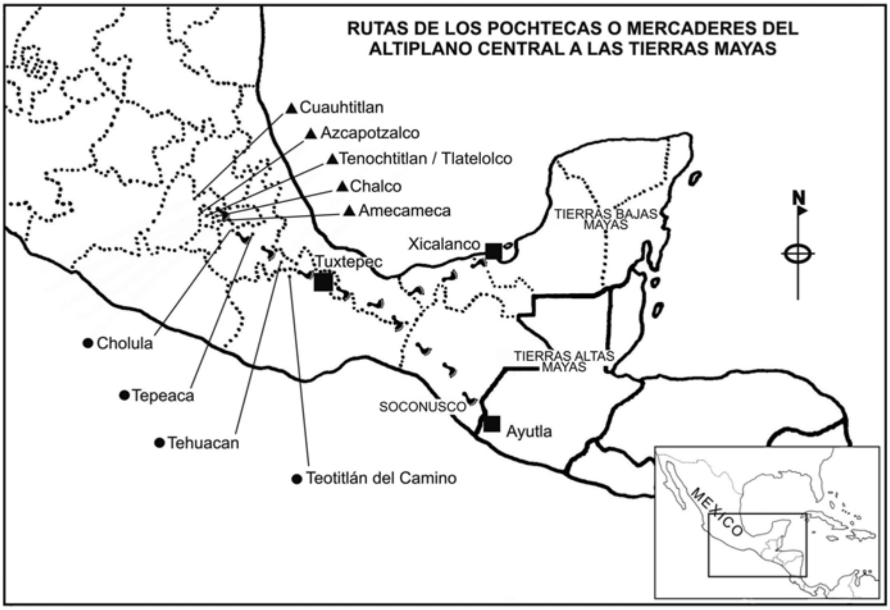

Fig. 7.1 Reconstruction of trade routes of the *pochtecas* [17]. The *black boxes* (▪) indicate major commercial localities under the influence of *pochteca* authorities from Tonalámatl. Based upon Arqueología Mexicana Ed. Esp. 18, p.10 (information of S. Reyes, drawing F. Villegas)

> Besides the Maya established a system of exchange with other peoples of Mesoamerica in the region of the Gulf of Mexico named port of trade (area where merchants two political entities came together to share their own territories products). Among the most important ports were: Coatzacoalcos, Cimatan, Potochtlán, Champotón and Xicalango, where they traded with the pochteca in the Gulf of Mexico, and Nito at the mouth of Lake Izabal and Naco in Honduras.

In the Maya area there were three regions of niche marketing: Yucatán, Tabasco and the Gulf of Honduras. The northern lowlands of the peninsula was used for the production of food for the daily diet, cotton, honey, *copal* (*pom* in Maya) and salt, which was the main resource Yucatán produced for trade. The southern lowlands meanwhile (Tabasco and the Gulf of Honduras) covered Chontalpa, among others. The strategic location of the Chontal gave them leverage over a vast system of water routes through various rivers to the Laguna Términos, which was vital for expansion and trade (apparently from the Preclassic to Postclassic, based upon archaeological remains). As a consequence, the Chontal became traders per excellence. It appears that a group of *pochteca* permanently settled there in order to trade for precious green gems and *chalchihuite* [14].

West Mexico

In western Mexico, the Purépecha (also reported as Tarascan) established a great empire that dominated this region of Mesoamerica. They developed commercial circuits in the region [10]:

> The market was seated in Tzintzuntzan, which supplied food and luxury goods to the residents of the capital. There was another market on the southern shore of the lake, near the present town of San Pedro, where island fishermen from Jarácuaro and farmers from Ihuatzio came. In this market, local specialties were exchanged. There was also a *tianguis* west of Tzintzuntzan, in Azajo, between the mountains and the lake, as well as in the northern subregions.

The Purépecha expanded their territory in order to obtain resources from the lowlands and the highlands. The conquered villages became interchange points along the trade routes as well as sources of tribute in the highland regions, where such market centers as Uruapan and Tacámbaro were founded [10].

Although hostility existed between the Purépecha and unconquered groups, trade over long distances flourished. Important products included rare and very prestigious metal jewelry, shells, and delicate colored pottery. The track to the northeast permitted access to shells from the Gulf of Mexico and certain Huastec and Totonac artifacts Purépechan products, such as cotton fabrics, have been recovered from sites in Tenochtitlan. On the other hand, Yucatan earrings were manufactured from Purépechan copper [10].

Virreinato Period

Up to now, we have analyzed different forms of marketing that existed in pre-Hispanic times. Central markets and local *tianguis* were supplemented by distance commerce and tribute systems established the Triple Alliance, with specialty products and raw materials derived from 42 provinces located in different ecological zones. The provincial suppliers provided food (e.g., beans, maize, peppers, amaranth, etc.), cotton textiles, among many other items used in everyday life as well as luxury items. After the Spanish conquest, certain basic commodities continued to flow into central markets, other products lost their value such as various types of shells and feathers.

The Spaniards were amazed by the variety of materials and products that were traded in different markets (e.g., Tlatelolco) and attest to the continuity of the importance of markets at the start of the Viceroyalty period. Francisco Hernández, described large aggregate of plants and animal products, metals among other goods that are still important in today's local markets [18]:

> … herbs, leaves, flowers, roots and seeds are used in medicine and in the food and in the fields; even the boys themselves, driven by the violence of disease and hunger, [use] … many little plants they know and are placed on sale, as well as [plants that] … kill and repel bed bugs, lice, fleas, mosquitoes and flies… the numerous indigenous fruits cannot be listed… one that has the greatest appreciation is the *cacahoatl*. Pigments are manufactured from flowers, fruit, roots, leaves, bark, stones, and woods, among others. Also there is much

> honey, cane juice from cane, maize, *maguey* and other trees and fruits. Other products include chia oil, torches and ixtle fiber, among other products more.

"Alcabalas" *(Sale Taxes) and "Relaciones Geográficas"*

Eventually Viceroyalty supply policy changed in New Spain and was regulated by the Spanish Monarchy. Novohispano markets operated under the strict surveillance of the representatives of the Crown in order to provide sustenance for the people as well as to stimulate domestic demand. The sales taxes, known as *alcabalas*, generated income for the monarchy.

Some regions of New Spain had more information from *acabalas* than others. In particular studies using data from Valley of Toluca, Oaxaca, Tlapa, Puebla–Tlaxcala region, Guadalajara, Tepeaca and Zamora demonstrate a general trend. The production and marketing of indigenous products became limited as the monopolist and associated intermediaries overtook the farms of indigenous peoples [19]. In the Huasteca region of the Gulf of Mexico, there is little information on indigenous participation in trade networks based upon *acabalas*.

The resources provided by the provinces were recorded the Relaciones Geograficas, official census conducted between 1579 and 1585. The questionnaire dealt with different aspects of life and economy and was distributed throughout the Spanish Empire by King Philip II. The earlier version consisted of 50 questions but was later reduced to 37 [20]. Although trade was not specifically quantified, plant and animal goods produced in each region were registered.

Another important trade center was the Valley of Toluca through which passed goods derived from Acapulco and Michoacán to the south [10] and from the Bajío to the north [21]. In addition indigenous goods were traded locally. The *alcabala* administrator of Toluca, Miguel Valero reported in 1777:

> … Indigenous people derive over half of their needs locally in the town of Toluca.

Most of registers include textiles, salt, beans, chilli, and livestock and not non-timber forest products (NTFPs) [21].

Routes of Marketing

During the Viceroyalty period [22],

> …exchange circuits, included routes to western Mesoamerica of New Spain to New Galicia, were not bounded by administrative politics of the kingdoms of New Spain's Viceroyalty boundaries. The juxtaposition of the land and socio-economic relations among centers of production or distribution centers as well as supply corridors had greater weight than jurisdictional boundaries established by the colonial administration.

The paths travelled in ancient times by *tameme* (porters) and *mecapalero*, are almost the same as those followed by the first orders of religious missionaries in the spiritual conquest and that later became the *caminos reales* (royal roads) which were transited by pack trains carrying commodities, precious metals, and manufactured articles both in New Spain and its provinces [19].

The city of Valladolid (now Morelia) was one of the important commercial centers of Michoacan, where pack trains from the hot lands arrived with the supplies that were dispersed by mule trains to Guanajuato, Celaya, Salamanca, Salvatierra, Irapuato, Queretaro, and San Luis Potosi, among other highland mining towns of the *tierra adentro*. Another important *camino real* passed through Mexico to Guadalajara, Morelia, and Pátzcuaro [10].

The major trade routes initiated in the City of Mexico and headed: (a) west to Querétaro, Zacatecas, San Luis Potosi and Parral; (b) south to Puebla and Oaxaca; and (c) southwest and southeast to the two ports of entry and exit of products, Acapulco and Veracruz. The viceroyalty cities were related to a vertical axis named *Camino Real* over which circulated the silver between the northern and southern poles of the Viceroyalty [23].

During this period, the mule train was the key to the transportation system for goods which were also carried on the backs of Indian porters (as was the case of the *tameme* of the past). The most important routes spanned several cities and distribution centers; the *camino de la plata* (silver path) or *Camino Real Tierra Adentro* (Interior Royal Road) radiated from the City of Mexico to connect the capital to the distant provinces of New Spain [15].

Rivers and lakes of central Mexico facilitated water transport of goods throughout lake system around Mexico City and its surrounding agricultural regions. Examples include the Chalco region that was known for its high productivity of maize and wheat as well as the Xochimilco area with vegetables and grains that were floated northward in the Viga canal to the capital. In the southeastern New Spain, the pre-Hispanic waterways of the Coatzacoalcos River served Veracruz and Tehuantepec while the Usumacinta and Grijalva Rivers articulated the regions of Tabasco and Chiapas, which remains active today.

The development of centers and routes for supply and trade during the pre-Hispanic and Viceroyalty periods are the basis for understanding the current market systems, their organization and operation. Many of the indigenous *tianguis* have survived certain impairments over of time and currently persist as important centers of assemblage and exchange of local and regional products, where prices are fixed according to local and regional production, regardless of the price of central markets.

Mexico Independent Period

Alcabalas, Reminiscent of the Viceroyalty

During the Independent Mexico period (particularly the end of the Viceroyalty period and early Independent Mexico in the early nineteenth century), a number of new *alcabalas* or sales taxes on certain products (e.g., sugar, grains, and animals) were implemented. However, these tax records do not identify ethnobotanical products of interest (such as NTFPs, gathered or cultivated plants, native fruits, or medicinal plants) because they were all grouped under one term *productos de viento* ("products of the wind") and recorded by volume. Consequently, this "other" category makes it difficult to determine their diversity and importance. None the less, a great volume of such products as sugar, wheat, textiles and spirits are recorded at checkpoints of regional markets in the eighteenth and nineteenth centuries [24].

Supply Circuits

In the case of the sale taxes on supplies for the city of Puebla in 1822, maize was not exempt from taxation. In general, goods of agricultural origin (e.g., flour, chilli, and beans) which undoubtedly had a great trade importance were not included [25].

Other very important supply circuits during this period were those serving Mexico City. However, it is difficult analyze these marketing networks. For instance, products of chinampas transported by the canals to the center were not taxed; hence, there is no record of the amount or range of products provided from the southern portion of the Valley of Mexico. A similar situation existed for products derived from local forests, such as coal and wood. None the less, various domestic products from Morelia such as cheese, rum, chilli pepper, salt, shoes, copper, sweet potato, *flor de tila*, and *muicle* are reported [24]. It is worth noting that *flor de tila* (*Ternstroemia* spp.) and *muicle* (*Justicia spicigera*) are the few medicinal plants recorded, suggesting their cultural importance over a wide region for at least two centuries.

Influence of Railway in Marketing

Late in the Independent period, the change of the transportation system began to alter the diversity of marketed products. As of 1873 the rail network began to expand with subsequent modification of the influence of colonial road networks on the distribution and marketing of goods. Before the construction of the railway network in Mexico, people and goods travelled overland along a network of roads and trails inherited largely from pre-Hispanic times. Between 1881 and 1910, the Mexican railway system grew exponentially from 1646 to 23,346 km [26] (Fig. 7.2). The rail network linked the productive regions of the country and permitted the effective and timely transport of many goods to several *tianguis*, some of which persist to this day along the railways. In addition to the delivery and exchange of goods, producers and sellers used the services of second class passage to optimize their transfer times [27]. Rather than carrying their goods on foot or by donkey to distant peripheral markets where they were sold at low prices, rail travel permitted timely access to central urban markets where they obtained better prices (oral communication: Abraham Mirafuentes, medicinal plant producer, Ozumba *tianguis*, November 25, 2003).

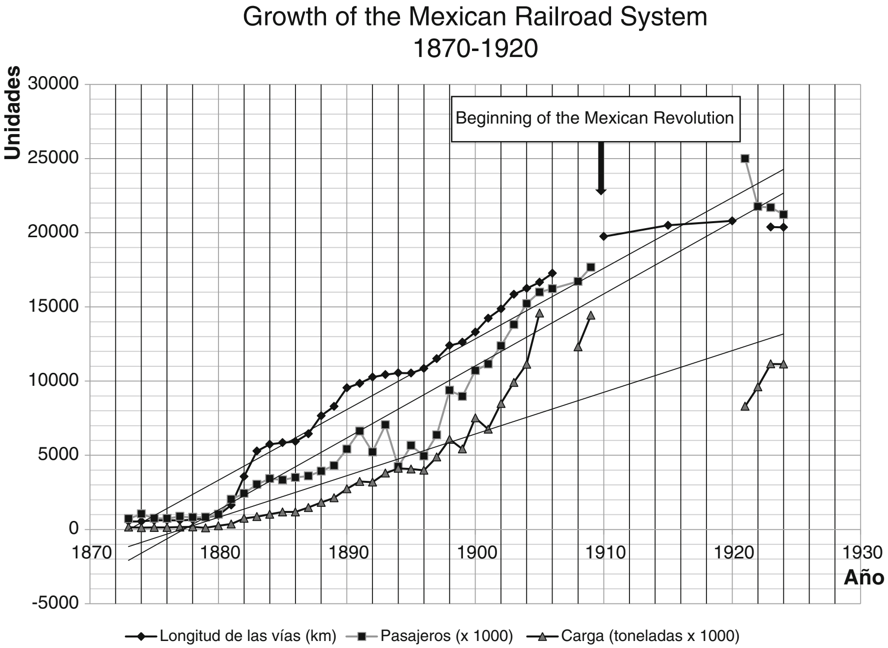

Fig. 7.2 Trends of growth of the Mexican railroad system between 1870 and 1920

Contemporary Period

Current Trade Heritage and Traditions

To this point, emphasis has been placed on the importance of studying the history of commercialization routes as well as *tianguis* and central markets in order to appreciate contemporary patterns and relationships in marketing useful plants. For example, in pre-Hispanic times, the tribute routes paralleled the trade routes. Trade corridors facilitated the movement of plant products from the west coast to the east coast (and vice versa); such reciprocal flow also existed along the north–south axis.

Pre-Hispanic exchange routes included roads and main market places [14, 16, 17]. Some of these courses and places have persisted in their importance, despite the changing marketing trends since then because of their strategic geographical location. This is particularly evident in the collecting and trade of medicinal plants derived from the tropical deciduous forest [28]. The contemporary market system of Mexico is the consequence of a long process of integration, evolution, and adaptation. The *tianguis* and market continue to be strategic focal points for evaluating society, economy and production systems which impact the relationships between plants and people.

Exchange of Products

The organization and interregional exchange of products persist in today's trade. The *plazas* and *tianguis* of Oaxaca have been the focus of classical studies that have documented the scheduled cycle of markets and the complementary of goods among ecoregions [6, 29]. Another example is the major *tianguis* of Ozumba, State of Mexico, located near Amecameca, a major pre-Hispanic crossroads. Within its areas of influence region, local *tianguis* in nearby communities are held on different days of the week and vary in terms of altitude and climate. For example, goods from "hot country" (in this case, Morelos) are exchanged from products from the "temperate country" (in this case, State of Mexico and Puebla). From the peripheral market center of Ozumba, the central markets of Mexico City take delivery of medicinal plants in Sonora Market, of edible mushrooms in the La Merced Market, and of various tropical and temperate fruits in the Central de Abastos (the major food supply center) [30].

The *tianguis* is important as a center of resource concentration and redistribution, where many products from different ecological zones converge. This type of *tianguis* has been referred to as primary *tianguis* [29], regional market centers [10], central *tianguis* [30] as well large *plazas* or large *tianguis*. Feeding into the primary *tianguis* are lower order *tianguis* [31], intermediate market centers and local market centers which are of smaller dimension, are less diverse and depend upon the primary one to provide commercial products.

Contemporary Studies of Markets

Markets provide a window of opportunity for ethnobotanical studies [32]. Hernández Xolocotzi [33] call attention that :

> the markets are the materials that have resulted from varying domesticating efforts of indigenous people … here is the great germplasm bank.

Since the 1970s, ethnobotanical studies have documented plant resources in the *tianguis* and markets of Mexico. Inventories have registered taxonomic diversity, forms of transformation, variety of uses, manners of applications and geographical distribution.

In addition, the plants present in the market places reflect different collection strategies, diverse management of ecosystems, as well as incipient domestication. An array of plants (and fungi) can be found that are employed for edible, medicinal, fodder, dyeing, textiles, construction purposes, among others. This range of products results from several interactions between humans and plants that occur in different environments under varying management regimes. Because traditional uses are consequences of interactions over time, history is inevitability linked to past, present and potential sustainability.

The contemporary *tianguis* is "a dramatic and temporary museum day" where one can study people, their material objects, values, and customs [31, 34]. In addition, it is a location from which one can document the distribution and sale of cultivated and wild plants, whether exotic or native to the region, discover the genetic variability of crops, learn different uses of which plant resources, as well as the economic relations and socially established between buyers and sellers [35].

Since the early 1970s, the mercantile circuits of Oaxaca have been studied extensively. Several studies in economic anthropology have focused on the contribution of regional products as well as the impact of exotic products. Some authors [5, 29, 36] have predicted economic imbalance if the regional markets are not maintained. Some changes in the regional markets are underway primarily due to lack of regional labor forces, migration, and rural depopulation.

Tianguis and Product Distribution

The current location of the great traditional markets reflects past interregional relations [37]. Due to the ease of transporting goods from the country side to urban centers by rail since the 1880s, many *tianguis* are located near former train stations, such as Ecatepec, Tlalnepantla, and Ozumba in the State of Mexico as well as San Antonio el Progreso (Municipality of Tepexi de Rodriguez) [6] and Honey in Puebla. In recent years, some market sites have moved to roadsides and intersections, which are more accessible by trucks and cargo vans. As a consequence, the diversity and quantity of manufacture goods have overtaken the regional products. These large *plazas* attract more outside buyers. For instance, at the *tianguis* in Ozumba, State of Mexico, buyers of medicinal plants come from surrounding highland states at specific times of the year to purchase different *copales*, which are in turn brought to Ozumba from the "hot country" from the south (Fig. 7.3). This traditional copal network has existed for at least three generations. Buyers at the Ozumba *tianguis* and similar markets are able to purchase an assortment of plant products that are concentrated from faraway places with different environments and flora. On a larger scale, wholesale buyers of medicinal plants from throughout Mexico make their purchases in the Sonora Market in Mexico City rather than in regional markets because at this central market "you can get all you need." It is inefficient and too costly for them to link up with distant regional market from their homeland.

Product Collection and Marketing

Biological materials derived from forests which do not require harvesting trees are known as non-timber forest products (NTFPs). Usually they include products that are traditionally gathered such as wild fruits (medicinal, edible), medicinal plants (especially bark, roots and herbs), *ocote* or pitch pine, *copal*, fungi, palms

Fig. 7.3 (**a**) Different clases and qualities of copal are sold at Ozumba market, State of México for the Day of the Dead. (**b**) Some of the vendors still use the traditional balance; in some cases a one kg comercial bag of soap poder is used as a counter weight. Author´s photos

among others. In many rural areas of the Mexico, such collection is the basis of a community's economy. The family income is supplemented by such products as *amate* bark paper [38] and aromatic *lináloe* [39].

Effect and Risk of Harvesting on Natural Populations

In Mexico, the plants, fungi, and animals are protected by national laws, in particular NOM059-SEMARNAT (Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo), which provide guidance for the exploitation of species that might be considered. One of the factors that can drastically decrease the abundance of a plant species is the overcollection. In addition to these regulations, the Ministry of the Environment (SEMARNAT) has established official criteria with respect to harvesting NTFPs [40].

Unfortunately, most wild plant collectors are uninformed about the regulations, a situation compounded by the fact that some are illiterate. In addition to the extraction of NTFPs for the market, many rural families and indigenous groups incorporate these plants into their subsistence practices and rituals, such exploitation is legally permitted.

Now that certain products and handcrafts have gained national and international recognition, the demand for raw material necessitates modifications in the plant's management and exploitation permits for the escalating commercial extraction. Such a permit includes a management plan that must be approved by the forestry authorities [41] as is the case of bark for *amate* paper, wood for *olináloe* and *alebrijes* of Oaxaca. Because these requirements are complicated, they are usually ignored by members of rural communities which have traditionally harvested from these resources for generations. Often the gatherers are more familiar with the local distribution and availability than the forestry authorities. In many cases, they sell the NTFPs in the *tianguis* without official permits.

Many of NTFPs in Mexico, especially medicinal plants and mushrooms, are voraciously collected as if by “ants” in order to generate supplemental income for the family’s weekly maintenance from the sale or exchange in the weekly *tianguis*. In this type of trade involves the whole family, including children. Plants are gathered in the surrounding forest. Men are responsible for the obtaining roots, bark or wooden splints. Women (accompanied by the children) gather the herbs near the village, in cultivated fields, and in home gardens. The small-scale collection is a common routine among many families in different regions of Mexico. In the case of medicinal plant vendors at the Ozumba *tianguis*, each week about 150 families offer medicinal plants and the number is growing. In other regions such as the “hot country” of Puebla and Guerrero, the number of collectors-vendors are decreasing due to emigration [42].

There are few quantitative studies on the influence of harvesting in the wild and on demographic aspects of natural populations that allow one to assess the conservation status of marketed plants [38, 43]. Studies in Tehuacán Valley, Puebla, have shown [8]:

> … That species with higher risk index value are the native plant species that are exclusively gathered. Commercialization of plant products in the traditional plazas is an indicator of a particular level of ecological risk, but these plazas are not the only ways that native plants arrive at the markets.

The risk to native plants and their conservation could also be related to the routes along which they are sold. In a study of edible flower buds, *cacayas* (*Agave kerchovei*), in the Tehuacán, Puebla, where they are eaten locally, traditional ethnobotanical research is integrated to establish a management plan that includes conservation of resources and ecological services [44, 45].

The regional collectors that supply various central markets in Mexico are unaware of the conservation status of species even if the local collectors detect a plant’s decreasing availability. For example, a study [46] conducted in Tuxtla Gutierrez, Chiapas, encountered 325 species of plants present in five markets. Using the standards of conservation status of NOM059-SEMARNAT, 17 species (used for ornamental, ritual, religious, ceremonial, medicinal, edible and handcraft purposes) were categorized as at risk; 11 species were endangered, 2 species subject to special protection, and 4 were endangered species.

One of the species listed in category of Special Protection is *árbol de la víbora* or stick snake (*Cyathea fulva* and possibly other related species). This slow-growing tree fern is present in markets, *tianguis* and Lenten fairs; the escalating sale of the trunks may drive this species to extinction. In the case of Tehuacán, Puebla [8], the highly prized medicinal plant, *Clinopodium mexicanum*, is considered to be over collected but is not listed in NOM059.

In Mexico there are at least three patterns of people’s response to overcollection of medicinal plants. First, people collect seeds, cuttings, or roots to propagate the plant. These are planted on a small scale in home gardens and later expanded in cultivated fields. Such is the case of Mexican arnica (*Heterotheca inuloides*) and

Mexican hyssop (*Agastache mexicana*) that are now cultivated in the area of the Sierra Nevada of central Mexico. Second, new collection sites, usually further away, are sought. Such are the cases of medicinal roots and barks as cancerina, (*Hemiangium excelsum*), valerian (*Valeriana edulis s*ubsp. *procera*), and copalquín (*Hintonia latiflora*). In the case of present-day palm handcrafts and construction, the raw material is derived from populations located at greater distances from the residences of the craftsmen than in the past [47, 48]. Third, the original species is replaced by a substitute plants which has similar characteristics. Such as the extraction of fig bark (*Ficus* spp.) to make *amate* paper decimated the local population of figs near San Pablito, Puebla, today, the bark of trema (*Trema micrantha*), *is* commonly used for the manufacture of "amate" crafts [38]. Other examples are the medicinal plants complexes: when the signature species considered the most effective is not available in the market, the subordinate members within their geographic range of distribution take their place [49].

Ocote, a Gathered Resinous Forest Product

The marketing of pitch pine called *ocote*[1] has deep roots and is still an important article of trade. In the past, it was also a currency used to pay *plaza* taxes because of its durability, ease of storage, and constant demand. The extraction of *ocote* is hard work, usually done by men, and, in some places, dangerous because it is illegal (which has slowed its extraction to a lesser degree) (Fig. 7.4). Eventually, the firing and carving base of the pine tree lead to its collapse and death.

Fig. 7.4 The extraction of ocote is a hard work that includes burning the tree trunk prior to cutting. (**a** and **b**) cutting and collecting charred wooden fragments which are rich in resin, and (**c**) sale of ocote in the market with other pine forest products. Author´s photos

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[1] Wooden resinous splinters extracted from different species of pine (*Pinus* spp.), that are used to start fires as well as medicinally.

The *ocote* in the *tianguis* of Ozumba (State of Mexico), Zoogocho (Oaxaca), and other regions of Mexico is supplied by various communities located in pine forests where it is offered by the *ocote* collectors; because it is inexpensive, there is no large resale market [5]. The sale of *ocote* "is like going to the bank to get cash" because the collectors supplement their market cargo (of other plants and animals) with it; if their seasonal products do not sell, at least some income can be derived from *ocote* (for which there is a constant demand) in order to cover the weekly household expenditures that occur in the *tianguis*. They usually maintain a reserve stock to which unsold bundles are returned. In addition, *ocote* is frequently bartered for tortillas, bread, or fruit.

Edible Plants

Among the most prized edible plants are *quelites* (edible tender greens), many grow spontaneously in anthropogenic habitats (e.g., cultivated fields or disturbed areas) from which they are gathered; in some case they are cultivated in small plots or home gardens. Cultural preferences and biological diversity of *quelites* vary from region to region. In *tianguis* of central Mexico, some of the preferred edible greens include: seepweed (*Suaeda edulis*), purslane (*Portulaca oleracea*), *chivitos* (*Calandrinia micrantha*), violets (*Anoda cristata*), pigweed (*Amaranthus* spp.), goosefoot (*Chenopodium berlandieri* subsp. *nuttalliae*), and *chepiles* (*Crotalaria longirostrata*).

Other species are gathered from wild plants and may be restricted to certain times of year such as edible flowers, including *gualumbos* or *hualumbos* (*Agave* spp.), *cabuches* (*Ferocactus pilosus*) (Fig. 4), *cacayas* (*Agave kerchovei*), *izotes or palmitos* (*Yucca* spp.), *garambullos* (*Myrtillocactus geometrizans*) and *matsitzes* (*Dasylirion* spp.) [48].

Mushroom

Ethnomycology has produced a variety of market studies on the gathering and selling wild mushrooms during the rainy season as well as their use and sale [7, 50–54]. Most data are derived from temperate forests while little is known about edible fungi of tropical zones [55].

Of the more than 200 edible Mexican fungi, over 100 are traded in markets [56]. The sale of fungi is based on traditional knowledge[2] whereby edible species have been selected over time. This knowledge has been kept in the collective memory of cultures and has been passed from generation to generation.

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[2] Traditional Knowledge: refers to innovations and practices of indigenous and local communities around the world who were conceived from the experience gained over the centuries and adapted to the local culture and environment.

Hongueros, people dedicated to collecting and selling mushrooms, know the specific sites in their forests for each species they market and return each year to collect them. However, many of them comment that the changing climatic conditions and forest clearings are affecting negatively the mushrooms distribution and abundance. Overcollection, usually by outsiders who invade the forests, has led to the decline of some mushrooms. Mushroom vendors in the Ozumba *tianguis* have commented that "there are not as many fungi as before," especially the most prized species.

Shift from Local Gathering to the Cultivation

Many plants sold in the central markets originate from various regions and communities. Fresh produce, especially for a specific dates (e.g., flowers for Day of the Dead or for Mother's Day), are cultivated near the central market. Other food products, which were formerly available seasonally, are sold year around due to post-harvest processing and effective transportation. Especially with agricultural products, Mexico's markets are now part the globalized economic system. For instance apples from around the world are found in the local markets, even in such traditional Mexican apple production areas as Zacatlán (Puebla) and Cuauhtémoc (Chihuahua). According to Hirth [3], the distance from where the resources are brought or where the products were exchanged is a measure of consumer demand. The shift in plant management from gathering to cultivation within the area of influence of the central market also reflects the impact of consumers.

In the case of Mexico's central market for medicinal plants, Sonora Market, many changes have occurred while some patterns have persisted. Production areas have expanded and some plants that were gathered formerly in the wild are being cultivated. The major areas of production and gathering areas of fresh plants in this central market originate from nearby regions. Local traditions have reinforced these activities and the movements of vegetal goods retrace pre-Hispanic trade routes. Woody plant products are still derived from wild plants such as *copales* (resins derived from *Bursera*) that pass from the Mixteca of Puebla, through local tianguis and main plazas as Ozumba before the Day of the Dead and, into the central market, Sonora Market. A similar pattern is found with dried medicinal roots, woods and barks for which large wholesalers strategically located in different biogeographic zones of Mexico develop a supply network of local dealers to satisfy the high demand of major markets of Mexico [57].

In the case of herbaceous medicinal plants, the trend is different. Farmers within the area of immediate influence of the central market are bringing into cultivation high-demand remedial herbs. In some cases, the local plant populations have diminished to such a degree that propagation material must be brought from distant areas. The provisioning of locally gathered wild Mexican arnica (*Heterotheca inuloides*) for the Sonora Market declined to such a level that consignments of plants from distant states of Michoacan and Puebla were needed to satisfy the market demand.

Agricultural producers of the Ozumba *tianguis* (about 70 km away) seized the opportunity grow arnica throughout the year. Ironically, they obtained seed from these distant plant populations. Even though the arnica grown in the Ozumba area is the same species, the populations appear to be of hybrid origin reflecting different genetic lineages of three varieties: *H. inuloides* var. *inuloides* (found from Nuevo León, Durango and Veracruz, to the State of Mexico), *H. inuloides* var. *rosei* (native to Zacatecas, Aguas Calientes, Guanajuato, Nayarit, Jalisco, Colima, and Michoacan), and *H. inuloides* var. *viridis* (endemic to the region located in Veracruz, Puebla and Oaxaca). Apparently different lineages of arnica found in the 18 production areas have adapted to different growing seasons along the altitudinal gradient [30].

Plant Complexes in the Markets

When surveying plants in markets across Mexico, one often encounters taxonomically different plants that share the common name, uses, and characteristics. These vegetal goods represent human's adaptation to local plants (which may or may not be phylogenetically related but geographically separated) to meet their needs. These taxonomically distinct plants form a medicinal plant complex [49] in which the members share the same common names, comparable uses, similar morphological/anatomical features, analogous organoleptic characteristics and parallel bioactive principles or properties. The signature or dominant member of the complex is considered the most effective and is commercialized within and beyond the plant's natural geographic area of distribution. The subordinate members of a complex are used within their geographic range of distribution when the signature species is not available in the market. They may be considered a substitute for that dominant species when it is unobtainable.

An example of a medicinal plant complex is *matarique* which is prized for treating kidney ailments and diabetes and for which the signature species in *Psacalium decompositum* from mountains of Chihuahua [49]. This species had been sold in many markets across the country. When consumers cannot purchase *P. decompositum* in the markets of central Mexico, a local *matarique* (*Psacalium peltatum*) is substituted. Even though *P. decompositum* exhibited greater hypoglycemic activity than other members of the complex [58], its presence in the market has declined attributable to its scarcity due to overcollection.

The network of a medicinal plant complex allows collectors and vendors to respond to fluctuations in the availability of certain species at regional and national levels. The analysis of a network permits the identification of the trade routes. The investigation of the *matarique* complex permitted the reconstruction of marketing routes of wholesalers and retailers of medicinal that span from northern to southern Mexico; such a pattern has been elucidated for medicinal plant wholesalers of Jolalpan, Puebla [42].

Seasonal Fluctuation of Local Product Sales

One of the most important environmental factors that influence the abundance and marketing of agricultural products is the rainy season. Seasonality is expressed as the rainy and dry seasons or the hot and cold. Usually the market is saturated with a particular plant during its production season and its sale price is low. None the less, their sale in the local *tianguis* supplements the family income. Some but not all plants can be processed (usually drying) in order to offer them off season, usually at high prices per unit. The prominence of certain plants in the market can reflect the customer's needs. For instance, the cold season finds many marketed herbs for treating respiratory problems, while during the rainy season medicinal plants for gastrointestinal ailments abound. In general, there are a greater number of sellers in *tianguis* offering their products because they have easy access to the plants in the field or home gardens.

The supply and sale of market goods can vary as well according to cultural, social, and economic factors. The Catholic liturgical year which replaced the intricate Aztec calendar intertwines rituals, festivals and markets at different seasons (e.g., Advent, Christmas, Lent, etc.). These multifaceted celebrations with home decorations, Christmas adornments, *roscas* or special breads of Epiphany, *copal* incense and fragrant flowers for the Day of the Dead among other events require local products and imported goods that are available seasonally in the markets. In the state of Querétaro 67 species (mostly wild gathered plants) are used to decorate the houses during the holidays [59]. Such floristic diversity dedicated to season adornment has been documented in the *tianguis* of Oaxaca and Veracruz and is common throughout Mexico.

Civic festivities also require vegetal goods to embellish public places. For example, September 16 celebration (the declaration of the Mexican War of Independence), children's first day of school, mother's day, Children's Day among many other special dates require specific products that temporarily supplant the normal products (such as medicinal plants) in the *tianguis* [30].

The "Central" Market of Medicinal Plants

Mexico's principal central market of medicinal plants is the Sonora Market in Mexico City that reflect many of the patterns commented along this work related with distribution and redistribution, complexes of medicinal plants, seasonal products and social, cultural, and economic factors, among others.

It has been the focus various studies ranging from general inventories to documenting remedies for specific ailments. One of the first was the study of plants popularly recommended for the treatment of eye diseases [60]. A preliminary inventory was produced later [61]. The potential contribution of market studies to ethnobotany was outlined in an example illustrating the linkage between the Sonora

Market and one of is supply areas, Santa Catarina del Monte (State of Mexico) [62]. During the decade of the 1980s, there was growing awareness of the importance of diabetes in public health of Mexico. Popular conceptions of the illness and the plants used in treatments were recorded from the market [63].

During the 1990s, the studies continued to focus on fresh plants. Various university theses and publications with different approaches [64, 65] were produced. On the one hand, source areas medicinal plants were identified in order to study aspects of production, harvest, and marketing. Selected medicinal plant complexes were analyzed such as the 11 species of *quinas* and their marketing routes [66]. Inventories of the nearly 300 fresh medicinal plants along with their uses and risk of overcollection were published [67, 68].

During the 2000s, the relationship between source areas and the central market was considered [69, 70]. Attention was given to the inventory of dried medicinal plants, especially the woods and roots. Taxonomic identifications of market samples were corroborated with complete botanical specimens for comparing anatomical data [71–73]. The relationship between the peripheral urban markets and Sonora Market was examined for over 800 useful species including medicinal plants [74].

Various studies of the medicinal plants of Sonora Market have been conducted but much more basic work remains. This market is important not only because it is the largest, central market of Mexico for medicinal plants but also because it has received the most attention. Its contents and changes reflect the situation of markets around Mexico and serves as model for ethnobotanical studies of other markets in the country [62, 75–77].

Other Current Trends

Other fields developing in ethnobotanical market studies are the usefulness of plants and their nutraceutical potential, based on phytochemical–pharmacological studies that diversify the applications of medicinal plants [78, 79]. The search for alternative management protocols of threatened or overexploited plants are important to guarantee their present and future use. An example of this type of study is that of *copalquín* or *copalchi* (*Hintonia latiflora*). With the increased demand for this traditional medicinal bark, most trees have been logged to facilitate debarking, a practice the essentially kills the tree. Recent studies demonstrate that the leaves contain same active ingredient and that its performance is higher in the pre-senescence stage; this information can be used to establish alternative production models to replace the bark with leaves derived from pruned trees [80].

Efficient production of wild medicinal plants brought into cultivation in order to meet the market demands requires the generation of horticultural knowledge so as to optimize crop yield. In the case of Mexican arnica (*Heterotheca inuloides*), the age (of 15 months) rather than pruning and soil fertilization was shown to produce plants with 60 % higher concentration of sesquiterpenes, the bioactive principles responsible for the inflammatory effect [81].

Final Comments

Studies of plants in local *tianguis* in Mesoamerica provide an overview of the management, collection and production in the area of influence of the *tianguis* or as Eder [4] states: "tianguis are microcosms that contain a representative set of regional environment in the local way of life."

Basic elements needed to understand the marketing aspects of a region include: (a) the history of marketing in the region; (b) the social aspects; (c) the changes that have occurred over time (routes, circuits, products, marketing chain, among others); (d) the impacts of current demands (through gathering, local production strategies), (e) the effect of the central market (e.g., pressure on natural populations); (f) the balance of local production; (g) the emerging demands for plants, especially for novel purposes (as seen in medicinal plant complexes and handcrafts); (h) the need for conservation of natural habitats; (i) the effect of marketing chains and the benefit for producers and gatherers; and (j) the regulations affect national and international trade.

All these are questions difficult to answer a priori and regional studies are needed to understand the difficulties and predict problems of species extinction. In cases where marketing threatens the very existence of a species, alternatives plants or management strategies are needed. The human element must be considered as well; the optimization of the marketing chain (by reducing the intermediaries and establishing just commercial relationship between producer and consumer) can reduce the over collecting pressure on natural populations and assure better family incomes.

Conducting ethnobotanical studies in local *tianguis* is challenging; most of the early work focused on biological diversity inventories and plant uses. When moving up to regional *tianguis*, more difficulties are encountered: Not only are basic inventories more laborious, but establishing a confidential relationship with buyers and sellers involves a multitude of interactions. Some of these are not readily obvious such as forms of exchange, type of transportation, and categories of sale. Finally, when the regional *tianguis* is linked to a central national market, the panorama expands with dynamic mutual relationships with local markets. As this level, research requires a range of case studies in order to illuminate the general problems and clarify the interactions that occur.

In recent years, the connection of *tianguis* with urban or central markets has generated unprecedented trade relations. Plant collectors have had to alter their strategies for obtaining the basic resource; in some cases, they drove the local plants to extinction, sought substitutes, or brought plants into cultivation, in order to meet the market demands. The consumers as well as governmental regulations add to the challenges that producer and vendors of ethnobotanical goods face.

If producers and collectors of useful plants are to survive in the evolving market system, Mexico needs to accompany them and support their progress. On one hand governmental regulations and conservation standards of NTFPs must take into consideration their livelihoods as well as the conservation of the plants. In order to support them effectively, basic and participatory research is required in order to generate a basis for technical programs that permit sustainable and optimal procurement of the raw natural materials.

Today's society is changing rapidly and, in some communities, the traditional knowledge is not considered to be important. However, much of the vegetation of Mexico and many of the domesticated plants are the results of millennia of interactions with humans. The traditional knowledge derived from such interactions is the key to understanding our forthcoming relationships with plants for the benefit of future generations, to respect our cultural heritage, and to fortify our cultural identity.

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Chapter 8
Ethnobotany for Sustainable Ecosystem Management: A Regional Perspective in the Tehuacán Valley

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Abstract Different indicators of global change identify that industrial processes are principal causes of the severe human impact on ecosystems of Earth. However, although industrial processes predominate in the world, numerous rural societies with a different rationality and organization coexist with the hegemonic mode of

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production. In indigenous communities the traditional botanical, zoological and ecological knowledge as well as traditional technologies of local resources and ecosystem management are particularly rich, as product of hundreds or thousands of years of experience. Indigenous communities have historically built diverse forms of managing the socioecological systems and the biocultural diversity adapted to local conditions, which are generally much more environmental friendly than other intensive forms of management. In this study we document the management of plant resources by peoples of the Tehuacán Valley, Mexico. We have inventoried more than 1600 plant species used for satisfying a broad spectrum of needs. People gather nearly 90 % of those species from wild populations, but practice different forms of incipient management (tolerance, enhancing, transplantation and seed sowing) in order to increase availability of nearly 400 important plant resources. The indigenous communities may adopt some modern techniques of managing resources and ecosystems, and select those according with their conditions and views. Based on these processes people construct hybrid techniques that may be adapted to the local environments. Agroecologists and ethnobotanists have visualized the high value of traditional management systems for generating technological viable alternatives for designing forms of sustainable management adapted to satisfy local needs and conserving biodiversity and ecosystems, and the continuous innovation tested by local people. It has been recognized that, in general, the traditional management systems have higher capacity for conserving biodiversity and ensuring the resilience of socioecological systems than industrial systems and that both traditional and modern techniques may contribute to better forms of management, but the form that the process adopts is crucial. Understanding traditional management systems are therefore the opportunity to reproduce valuable experiences, models and lessons for sustainable management and participatory adoption of new techniques may help to solve problems not traditionally solved. This chapter shows a general panorama of ethnobotanical information about resources and local traditional management strategies among Nahua, Mixtec, Mazatec, Cuicatec, Popoloca, Ixcatec and Mestizo peoples of the Tehuacán Valley, in order to analyse their role in designing a future for the region based on sustainability, an experience that may be useful for this and other regions of Mexico.

Keywords Ethnobotany • Sustainability • Traditional ecosystems management • Tehuacan valley

Introduction

Different indicators of global change [1–3] identify that industrial processes have been the main cause of the severe human impact on the planetary ecosystems. Nearly half of the natural ecosystems of the Earth have been drastically transformed in the last three centuries, but it has been especially accelerated since the second half of the twentieth century [2]. The future of the planet difficultly will be viable under the rhythm of intensification that has been the trend of the production systems characterizing the modern technological and economic models of development. The rhythms of the intensive agricultural and livestock production models of the last 50 years are not viable any more, since their technological bases (hydrocarbon based energy) would increase the impact on water, atmosphere and forest cover, which has already been catastrophic [4–7]. Looking for alternative technological and economic models is therefore a high priority for contemporary both science and society.

Although industrial processes predominate, numerous rural societies coexist with them in the World. In rural societies, particularly in indigenous communities, traditional botanical and ecological knowledge and technology are particularly rich. These communities have constructed historical forms of managing socioecological systems adapted to local conditions, and based on different principles to those of the contemporary industrial ways of life, generally friendlier with environment. These societies have adopted some modern techniques (either voluntarily or involuntarily), commonly selecting those that are useful from their perspective, and hybridizing them with their traditional experiences. Therefore, they have a valuable repertory of techniques that may help to face the contemporary and future problems of sustainability.

Agroecologists and ethnobotanists have been visionaries of the value of traditional management systems as technological alternatives for designing the future life, in order to reach goals of satisfying social requirements while conserving biodiversity and ecosystems functions [8–11]. It has been generally recognized that traditional management systems have significantly higher capacity of conserving biodiversity and resilience [12, 13] than the industrial ones. Understanding traditional management systems, therefore, offers valuable experiences, models and lessons for constructing sustainable management strategies.

We show in this chapter a panorama of our ethnobotanical studies on traditional management of biodiversity and ecosystems by the Nahua, Mixtec, Mazatec, Cuicatec, Popoloca, Ixcatec and Mestizo peoples of the Tehuacán Valley (Fig. 8.1), in order to analyse their role for constructing alternatives of sustainable management for the Tehuacán Valley and other regions of Mexico.

Research Strategy

The main theoretical interest of our research is understanding motives and consequences of interactions between societies and nature through management. We define management as deliberate interventions, transformations and/or decisions about natural and artificial systems, their elements (or resources) and/or their processes or functions (ecosystem services). Management is part of a general process of appropriation of the World by humans or the humanization of the reality. Use, conservation and restoration or recovering of systems, the resources and functions they contain are all expressions of management. For understanding management we support our research on theoretical frameworks analysing the articulation of knowledge, believes and practices of humans about the natural and artificial systems they manage. These aspects have been proposed as general principles of ethnoecology

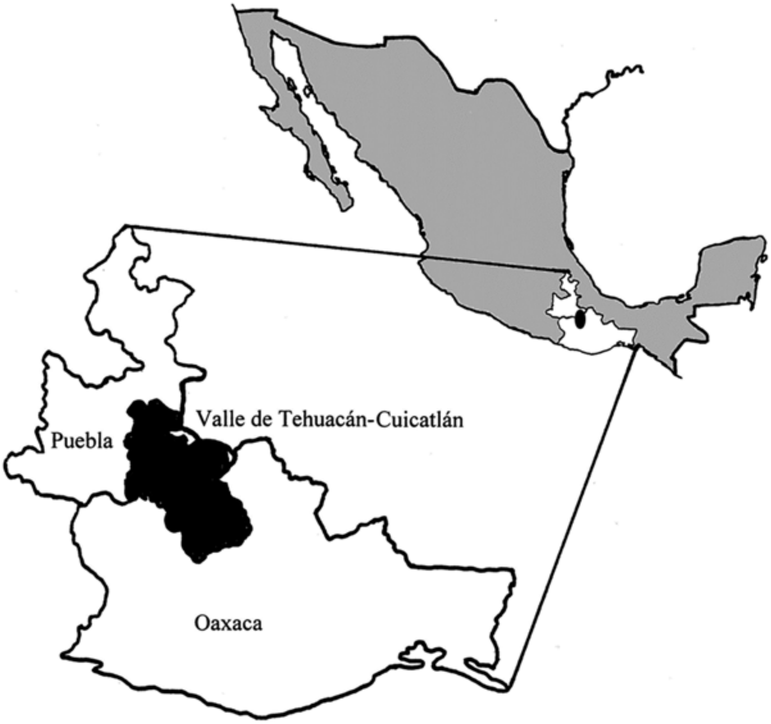

Fig. 8.1 The Tehuacán Valley in central Mexico. One of the regions of Mexico with the longer history documented of interactions between humans and plants, as well as one of the areas with higher ethnobotanical information. In this chapter we centre our attention in this region in order to analyse conditions of ethnobotanical research to connect its aims with those of other sectors of the society looking for sustainable use of natural resources and ecosystems

by Toledo [14], but we consider these are more general premises for understanding human culture and therefore we have adopted them for our ethnobotanical studies about plant management (Fig. 8.2). Also crucial in a sociocultural dimension of studies of plant management we should mention the understanding of how communities construct their agreements and institutions to accessing resources and ecosystems; in other words, how the commons govern their relation with nature and with themselves [15]. In addition, we consider highly valuable the perspective of the ecological economics that allows analysing the role of resources and ecosystems in reproducing the life of households and communities. An integral approach of all these aspects is crucial to an in-depth examination of how social processes influence management decisions and vice versa.

Another main perspective of our research is provided by the ecological theory. We particularly study the consequences of management on the structure and dynamics of populations, communities and ecosystems providing resources and services (Fig. 8.2). We look for understanding how distribution, abundance, diversity, and biotic interactions among organisms composing and regulating the managed systems influence the way humans manage both resources and systems [16]. One of

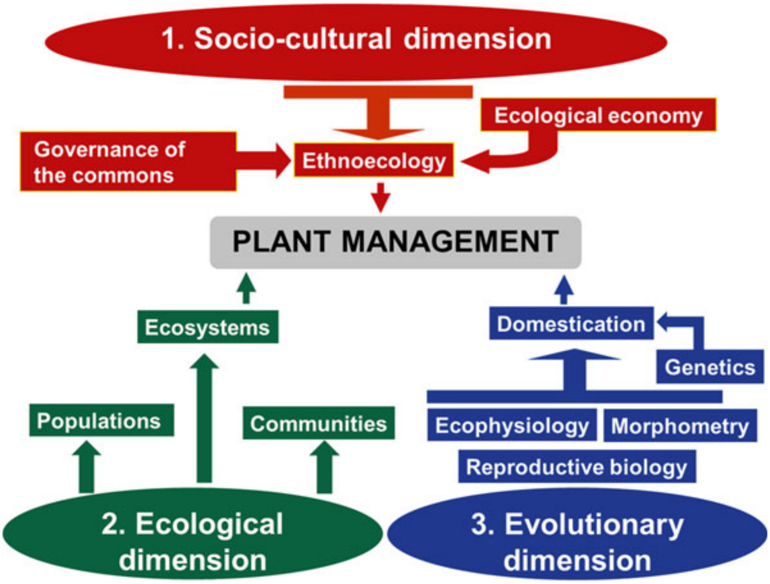

Fig. 8.2 General scheme of the strategy of our research group. The main aim of our studies is to understand processes that influence and that are influenced by human management of plant resources and ecosystems. We analyse management from three main perspectives: (*1*) The socio-cultural dimensión, mainly examining human cultural aspects such as traditional knowledge, believes and practices as established by the framework of ethnoecology, as well as social aspects related to the governance of the commons, through which we analyse agreements and institutions constructed by communities and regional instances for regulating access to resources and ecosystems, and economic processes relating the role of plant resources and ecosystems in the life of peasants' households and communities. We aim to analyse how articulation of knowledge, social agreements and interchange influence and are influenced by human management. (*2*) The ecological theories provides to our group a broad scientific framework to study the effect of human management on distribution and abundance of species, structure and dynamics of populations, diversity and interactions in biotic communities and ecosystem structure and functions. Also, we try to understand how these ecological aspects influence human management of natural resources and ecosystems. We particularly consider important these aspects to understand ecological motives of constructing technology, as well as to design strategies of sustainable management of plant resources and ecosystems. (*3*) From an evolutionary perspective we look for understanding morpho-physiological and genetic changes occurring in plant populations as result of human management. These changes allow analysing the variety of mechanisms and evolutionary forces intervening in modelling the genetic resources at present, in the past and for designing the future. In addition to this Darwinian approach for studying domestication, we look for understanding the connection of processes at scale of individuals and populations and those occurring at landscape level (landscape domestication) and vice versa

our principal question is what the ecological consequences of management are, as well as what the ecological requisites to construct sustainable management are. This approach therefore connects our studies with important paradigms such as sustainable management, ecosystem conservation and restoration, adaptive management and resilience of socioecological systems.

The third main dimension of our research is based on evolutionary theories, since management determine important evolutionary processes. We particularly analyse processes of domestication occurring at population level [17, 18], as well as those occurring at landscape or territorial levels [19–21]. We look for understanding the variety of ways the human cultures influence domestication, the mechanisms involved and their consequences. The Tehuacán Valley is an important setting for studying domestication because there is information about humans and plants from the prehistory are the processes are alive. We have in this setting the opportunity of connecting the past with the present for understanding the origins of the Mesoamerican civilizations, but also for designing the future of their lives.

Biocultural Diversity in the Tehuacán Valley

The Tehuacán Valley is a territory with biocultural diversity exceptionally high. It is a relatively small portion of Mexico, only 10,000 km^2 extent (Fig. 8.1); but there, it is possible to find there a great heterogeneity of ecosystems, represented by nearly 36 types of vegetation that have been called and described as "plant associations" by Valiente-Banuet et al. [22], as well as an extraordinary richness of landscapes conformed by patches of natural and artificial ecosystems managed for thousands of years [16, 23–26]. The region harbours a high biodiversity comprising more than 3000 plant species, 150 species of birds [27] and an also high richness of species of mammals and other groups of organisms [28]. In addition, the Tehuacán Valley is the territory of communities of Nahua, Mixtec, Popoloca, Chocho, Ixcatec, Chinantec, Mazatec, Cuicatec and Mestizo peoples [29]. Our research is directed to study the interactions of these traditional societies with the biological and ecological diversity of their territories, how and why these peoples construct their forms of management, the causes and consequences of their management practices on local resources and ecosystems, and how these practices may be used for constructing regional strategies of sustainable ecosystem management.

Diversity of Resources and Diversity of Risks

Our ethnobotanical studies have documented a regional inventory of more than 1600 plant species used by peoples of the region [29, 30]. This is a high number in absolute and relative terms compared with other regions of México (Table 8.1) and considering that in the entire Mexican territory it has been estimated the occurrence of 6000–7000 useful plant species [31]. We have documented on average 335 ± 130 useful plant species per community studied. The general inventory of plant resources of the Tehuacán Valley has identified 874 species used as fodder, 396 as medicine, 339 as food, 313 as ornamental and 209 as fuel wood, among the main uses [31]. Each species has on average 2.9 different uses ranging from 1 to 15 different uses per species.

Table 8.1 General floristic richness and richness of useful plant species in some regions of Mexico more intensely studied

Region	Vegetation	No. spp.	km^2	Spp./area		Source
Tehuacán	TSF	**1608**	10,000	**0.16**		[29, 30]
	TDF					
	POF					
Sierra Norte de Puebla	POF	720	13,000	0.06		[29, 30]
	CF					
	TRF					
Uxpanapa, Ver.	TRF	325	5000	0.07		[29, 30]
Selva Lacandona	TRF	415	13,000	0.03		[29, 30]
Sian Ka’an, Q Roo	TRF	316	5280	0.06		[29, 30]
Huasteca	TRF	445	–	–		[29, 30]
Región tepehuana	TRF	380	10,500	0.04		[29, 30]
Sierra de Manantlán	CF	650	1400	**0.46**		[29, 30]
	POF					
Tenejapa, Chis.	CF	645	–	–		[29, 30]
	POF					
	TDF					
Península de Yucatán	TDF	**1000**	140,056	0	0.007	[29, 30]
	TRF					
Montaña Gro.	TDF	430	11,000	0	0.04	[29, 30]
	POF					

Number in bold indicates the highest ciphers absolute and relative (in relation to the area of the region), respectively, recorded. *TSF* thorn-scrub forest, *TDF* tropical dry forest, *POF* pine-oak forest, *CF* cloud forest, *TRF* tropical rain forest

Undoubtedly this is an extraordinary inventory of plant resources that could support a broad spectrum of purposes, but improving life of local peoples should be the most important, as well as recognizing their intellectual property rights of such knowledge. However, not all plant species identified are equally important in satisfying human requirements. We have documented the annual consumption of species used as food, medicine and fuel wood, the amounts used, which ones are explicitly preferred by people and which ones are considered substitutable and which others do not. Some examples of the data obtained in the field can be seen in Table 8.2. These studies allow identifying those species on which humans exert the higher pressure and which ones, according to their scarcity or abundance, may be in higher or lower risk, respectively, because of their use. Details of these studies can be consulted in [32–36], among other studies.

Based on the sampling of the main useful plants as referred to in the paragraph above, we estimated that, out of the general inventory of useful plants of the Tehuacán Valley, nearly 11 % (about 170 plant species) are of particularly high use value. We find among them some species that have been valuable resources for thousands of years as demonstrated by the archaeological studies by MacNeish [37]

Table 8.2 Examples of data recorded in ethnobotanical studies in communities of the Tehuacán Valley

San Lorenzo Pápalo			
Species	Consumo promedio anual por familia (kg)	Frecuencia de uso (veces/temporada)	Índice de Mención[a] (%)
Quelites			
Yerba mora *Solanum nigrecens*	8.2	13	93.3
Quintonil *Amaranthus hybridus*	10.8	13	93.3
Berro *Roripa nastrurtium.officinale*	16.96	14	90
Papaloquelite *Porophyllum ruderale subsp macrocephallum*	2.74	31	73.3
Pepicha *Porophyllum tagetoides*	0.41	2	63.3
Verdolaga *Portulaca oleracea*	1.84	5	43.3
Quelite *Chenopodium berlandieri*	2.3	3.2	78.4
Frutos			
Pitaya *Stenocereus pruinosus*	65.5	8	87
Leña			
Encino cucharo *Quercus conzatii*	4436		100
Encino blanco *Quercus magnolifolia*	2594		100
Santiago Quiotepec			
Quelites			
Quintonil *Amaranthus hybridus*	3.0	8.1	92.9
Verdolaga *Portulaca oleracea*	3.0	5.3	89.3
Quelite *Chenopodium berlandieri*	2.3	3.2	78.4
Chpile *Crotalaria pumila*	1.0	2.4	63.4
Yerba mora *Solanum nigrescens*	1.0	2.3	46.3
Frutales			
Chonosle *Escontria chiotilla*	2.1	12.3	93.5
Pitaya *Stenocereus pruinosus*	2.0	13.1	90.5
Cardón *Pachycereus weberi*	2.0	11.7	90.1

Total amounts, frequencies of consumption and use preference of some species of quelites, edible fruits, and fuel wood recorded among households of the villages of San Lorenzo Pápalo and Santiago Quiotepec, Oaxaca (more detailed information can be consulted in Pérez-Negrón and Casas [33]). The information illustrates parameters used as indicators to calculate use value of useful plant species. Based on this type of information, from the general inventory of 1608 useful plant species we identified nearly 170 native species more consumed and appreciated by people of the communities studied

Note: [a]The index of mention represents the frequency of reference by people interviewed to the use of a species and it is also considered as an indicator of the use preference of the species. Valuing the use preference has been more deeply discussed in other studies of our research group.

and Smith [38]. These are for instance the cases of *Opuntia* spp., *Agave* spp., *Cyrtocarpa procera*, *Ceiba aesculifolia* subsp. *parvifolia*, *Sideroxylon palmeri* and columnar cacti (*Stenocereus* spp., *Polaskia* spp., *Pachycereus* spp., *Lemaireocereus hollianus*, *Escontria chiotilla*), among others.

Another approach for evaluating the importance of plant resources is the net of interchange and the balance between supply and demand (see for instance the study by [34]). In the Tehuacán Valley we have identified nearly 190 native plant species that are interchanged by cash or other products (barter) in the regional markets. Particularly important are plant species used as food, medicine, ornamental and fuel wood. Not all the species recorded in the markets coincided with the 170 identified with high use value in the communities, which indicates that both research approaches provide complementary information to identify crucial plant resources. Our sample of plant resources in six communities and six regional markets identified that about 210 plant species (nearly 13 % of all useful plant species identified in the region) are the most meaningful plant resources for local peoples, the ones that are more highly extracted, and those on which conservation policies should centre their attention.

We have analysed the magnitude of risk of plant resources associated to their use by documenting their ecological situation. Through vegetation sampling carried out in nearly 120 points (500 m^2 squares) of the region, we have estimated distribution and abundance of plant resources in most of the vegetation types of the Tehuacán Valley. We have also initiated a diagnosis of the structure and dynamics of populations of some of the most critical resources, in order to identify the critical stages of their life cycle for ensuring their permanence, which interactions with other plants and animals are also crucial, which plant parts are collected and the effect of collection on survival of plants and populations, among other aspects. The identification of the risk categories provides information for systematizing the scientific information available for species and ecosystems of the region, the ethnobotanical information about use and management, and identifying the priorities of research and actions for conservation. This information aspires to become protection policies promoted by the authorities of the Biosphere Reserve and those of the villages with critical problems, as well as for designing research strategies by the academic institutions.

Risk is a complex relation of ecological conditions, biological attributes intrinsic to each species, the part used by people, the level of intensity of extraction and whether or not people practice management to prevent its lose. In general terms, a scarce species with high extraction and no management is in higher risk than an abundant species under low pressure of extraction (Fig. 8.3). But also, risk is higher in those species in which the entire individual is extracted compared with those whose fruits or leaves are collected; it is higher the risk of practices affecting trees than those affecting herbs, it is higher the risk in plants depending only on sexual reproduction exclusively determined by specialized pollinators, compared with that of other species that combine vegetative and sexual reproduction and have generalist pollination systems. Among the social factors the cultural and economic value as described above are important, as well as the occurrence or not of communitarian organizational processes directed to decrease the risk, agreements, planning and actions, among other aspects. We have started efforts to systematize and classify

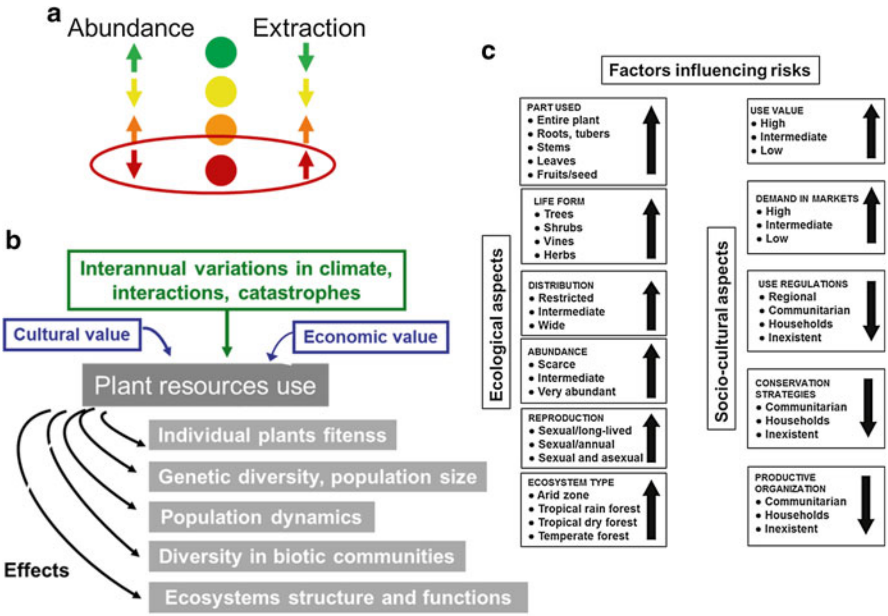

Fig. 8.3 Natural and sociocultural processes that may determine risk on plant resources. (**a**) A general typology of risk based on the balance between availability (distribution, abundance, temporal availability) and extraction rate of resources. A high abundance (*ascendent arrows*) and low extraction (*descendent arrows*) mean lower risk (*Green and amber colour circles and arrows*) of a resource in relation to its use; lower abundance and high extraction determine higher risk (*orange and red colour circles and arrows*). (**b**) Factors that may influence use of plant resources and effects that it may determine at population, community and ecosystem levels. (**c**) Factors that may determine increase (*ascendent arrows*) or decrease (*descendent arrows*) of risk availability and disappearing of plant resources

states of risk, since we find in these states critical motives of plant management that in theory could help to understand processes that leaded to the origins of agriculture and domestication (see the chapter 10 by Blancas et al. in this book). But also, studying the specific state of risk in particular areas of the region, and the ecological and social processes influencing it, provides useful information for constructing public policies and research strategies for guiding actions.

Diversity of Management and Domestication

Natural risks and those influenced by societies have historically influenced developing management techniques in order to decrease such risk. The practices include agriculture, which can be defined as cultivation of domesticated plants [19], but also a broad spectrum of forms of management that have been called “incipient management” by a number of authors since the practices involved are less complex than agriculture [19, 39, 40]. One of the most common and extended incipient management in the Tehuacán Valley is tolerance (Fig. 8.4), occurring when people clear a

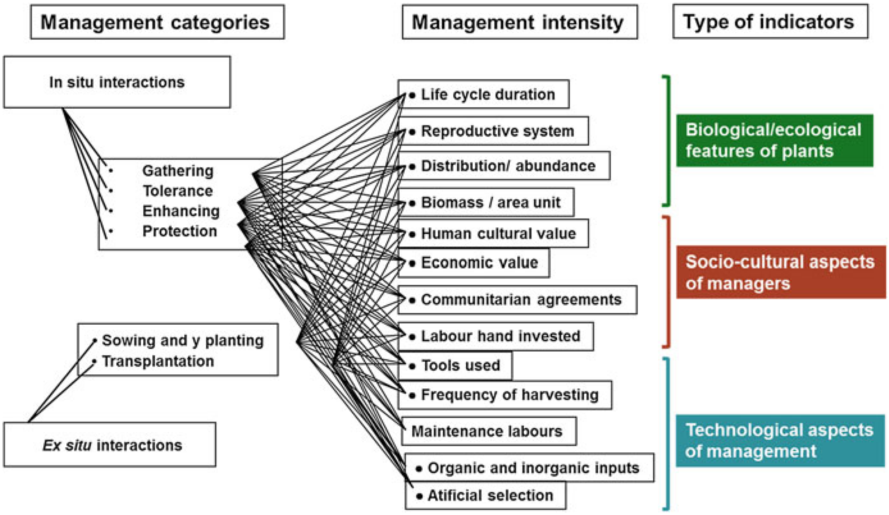

Fig. 8.4 General spectrum of management forms identified in the Tehuacán Valley. The general categories of management forms in situ and ex situ may vary according to their intensity influenced by biological and ecological, sociocultural and technological factors. All factors illustrated may have a variable condition which explains the broad spectrum of management states of plant resources. Modified from Blancas et al. [24]

patch of vegetation with different purposes and leave standing some particular plant species and phenotypes. It also happens with weedy plants in crop fields, when people practice weeding but let standing a variety of useful plants (for instance, quelites, green and red tomatoes, jaltomata, cucurbits, plants used as fodder, among others). Another management form is enhancing or induction, through which people deliberately propagate some plants to increase their availability. Some other plant species receive special forms of protection, such as removal of competitors, protection against herbivores or parasites, against shade or excessive solar radiation. All these interactions occur in situ; that is, in the areas where the organisms originally occur.

From the inventory of nearly 1600 useful plant species recorded in the Tehuacán Valley, nearly 1400 are obtained though simple gathering [24], but nearly 600 species receive one or several management types. The cultivated plants are under the highest management intensity. We have identified that nearly 57 % of the cultivated plant species in agroforestry systems of the region are native; that is, coexist with their wild relatives occurring in natural forests. This information, as discussed below, indicates that agroforestry systems are crucial for protecting an important fraction of the native biodiversity.

Other management forms occur out of the plants' natural environments (crop fields, homegardens, for instance) and these are called ex situ management. Figure 8.4 shows that the different categories of management type described above may occur at different levels of intensity, a topic that is discussed more deeply in the Chapter 10 by Blancas et al. in this book. The important aspect here is that taking into account the management type and intensity it is possible to find in the field a really broad spectrum of management conditions which deserves a deeper study to understand theoretical aspects of management and domestication but also to contribute to systematize an inventory of plant management techniques which would be of great value for making decisions for sustainable management.

One of the consequences of management (and we can say its final purpose) is domestication. Domestication can be defined as an evolutionary process guided by humans, mainly through artificial selection [17], but also through other evolutionary forces favoured by human actions, particularly gene flow, inbreeding, and genetic drift [21, 40]. The mechanisms through which domestication operates are relatively simple, but the human culture involved in the guidance of the process is highly complex. The real challenge in studying domestication is understanding the human cultural processes involved in selection, gene flow, breeding and genetic drift conditions. Although the evolutionary forces mentioned generally reduce genetic variation in populations, domestication has been historically recognized as a diversifying process [17], through which people generate new variants markedly different from others they derive from. Domestication is the main force modelling diversity of genetic resources. It is a continuous process which can be documented at the present allowing thus understanding the past; but it is also an extraordinary tool for designing the future of production systems. Today, conserving the process rather than particular varieties is maybe the best way to ensure the development of adequate responses for the risk that environment and production systems are facing at planetary scale because of global processes of change. We have studied domestication processes in different human cultural and ecological contexts, and a general panorama of these studies is shown in the chapter 11 by Casas et al. in this book).

Diversity of Ecosystems and Their Management

The main human activities associated to primary production involve diversity systems. It has been a long history of interactions between humans and ecosystems, as mentioned above. Throughout time, these activities determine risks on regional ecosystems, and we have identified the following as the most important in terms of extent and modification of original ecosystems: (a) the expansion of the agricultural area, (b) the extensive raising of livestock, (c) the extraction of fuel wood and (d) the intensive extraction of forest products for commercialization. We have identified some of the main plant resources that could represent technological alternatives for attending principal problems, as well as experiences of local management and perspectives of research and actions to control them.

Agricultural Frontier Expansion

The forests harbouring the high biological diversity referred to above, have historically been transformed in agricultural areas. The Tehuacán Valley is one of the most ancient sites of Mesoamerica practicing agriculture and clearing forest to establish agricultural areas is still a current practice. The alluvial valley of the Salado river was intensively used for agriculture since pre-Columbian times, as indicated by the intricate systems of channels and the great Purrón or Xalcatongo dam, one of the earliest hydraulic system constructed nearly 2700 years ago [37]. Apart from the agriculture of this alluvial valley, agriculture of the region is predominantly seasonal agriculture. The irrigated area is dominated by plantations of sugar cane but there are still remains of ancient intensive agriculture of maize.

From the beginning, agriculture of the Tehuacán Valley has been characterized for managing crops in a great variety of agroforestry systems that combine wild and domestic components. Forest, agroforestry systems and the secondary vegetation of fallow agricultural areas conform a landscape to a matrix of environments highly variable in composition. Agroforestry systems include the multicrop milpa system with and without irrigation, homegardens, and other agricultural systems and fruit plantations in which we have found a high diversity of managed plants [24]. Among the more detailed studies we can mention those of the temperate highlands up in the mountains [26], those of the arid fringe, the area of columnar cacti forests [23, 41], and the alluvial valleys of the Salado river originally composed mainly by mesquite thorn scrubs (Fig. 8.5). In these studies we compared the richness of species within

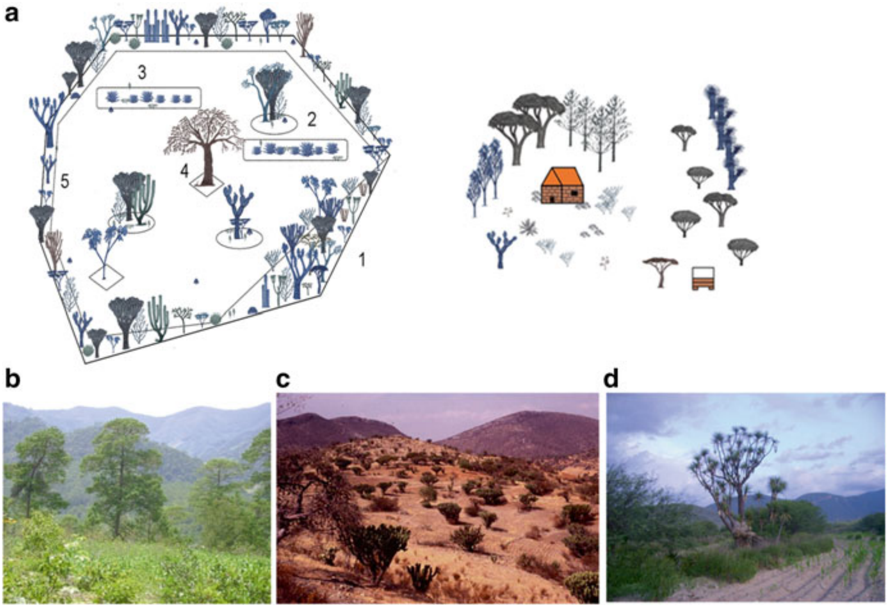

Fig. 8.5 Agroforestry systems of the Tehuacán Valley. (**a**) General scheme of agroforestry practices in milpa systems and homegardens. (**b**) General aspect of agroforestry systems from the highlands, (**c**) the arid fringe and (**d**) the mesquite thorn-scrub alluvial valleys. In (**a**) numbers represent agroforestry practices identified in agricultural plots. *(1)* represents a patch of vegetation left inside the agroforestry plot, (*2*) is a vegetation island, (*3*) a fringe of agaves used as barrier to protect against soil erosion, (*4*) is an isolated tree and (*5*) is a live fence surrounding the plot

agroforestry systems and that of the surrounding forests. Agroforestry systems of the highlands maintain on average 48 % of the perennial species of the surrounding forests [26], those of the arid fringe on average maintain nearly 54 % of annual and perennial plant species [23], whereas those of the mesquite thorn-scrub nearly 30 % [42]. Generally, there is a higher proportion of useful species in agroforestry systems compared with the natural forest, which indicates that one important criterion for let standing individual plants in cleared areas for agriculture is associated to their potential use. It is important to notice that at landscape level people leave and remove elements with principles similar to those described for favourable and unfavourable phenotypes of a species, respectively. This is an expression of domestication of landscapes in which not only composition but also other processes such as hydrology, soil erosion, may also be controlled [20]. It is also important to notice that processes of domestication based on management of individuals and populations of a species may significantly influence processes of domestication at landscape level; and similarly, actions associated to domestication at landscape level may significantly influence processes of domestication at population level. The connection of these two types of processes remains scarcely examined but it is an example of trans-scale phenomena associated to management of great significance for designing ecosystem management at regional scale.

Homegardens are other variable group of important agroforestry systems. In a recent study in the Tehuacán Valley [25], we found that homegardens maintain more than 350 plant species, 34 % of which are native to the region and on average 16 % of them are part of the forests surrounding the villages where the homegardens studied are settled ($N = 5$ villages). Although the information is still incomplete, the sampled areas studied show that agroforestry systems have an important capacity to conserve native biodiversity and that these are crucial systems to consider in all policies for regional biodiversity conservation. Such importance is particularly high because individual plants maintained in these systems are not isolated, but they also maintain interactions with other individuals and other species occurring in the surrounding forests. Among the important interactions documented we can mention gene flow through travel of both pollen and seeds. For instance, studies of population genetics of seven species of columnar cacti for which wild and managed populations in agroforestry systems coexist, we have documented levels of gene flow (*Nm* is a parameter in population genetics studies; in general, values higher than one are considered high) much higher than three among wild and managed populations. This information indicates that at least for the species studied, which are principal components of natural vegetation, agroforestry systems are important for the general maintenance of genetic diversity in wild, silvicultural and agricultural managed populations of the species studied. Also, the information indicates that the agroforestry systems are important reservoirs of biodiversity at both species and genetic variation levels.

Frugivory is another important interaction. Numerous plant species managed in agroforestry systems are consumed by complex communities of birds, bats and other mammals depending on these resources. Agroforestry systems contribute in the general maintenance of these communities at landscape level becoming real bridges between wild, secondary and used systems. The communities of herbivores are also benefited from the agroforestry systems. The diversified offer of resources contributes to buffer the effects of herbivores on crops; similarly the patches of natural vegetation contribute to maintain conditions for communities of pollinators that benefit both wild and cultivated components of the landscape. In fact, these interactions mentioned are considered important ecosystem services.

In addition, we should mention the role of trees and shrubs maintained in the agroforestry systems as nurse plants. Facilitation is widely recognized as a crucial interaction among plant species which become crucial in recovering of vegetation. Nurse plants provide shade, nutrients, protection against herbivores, humidity, mycorrhyzes, and other micro-environmental aspects that may be determinant for the establishment of a number of plant species, particularly succulent plants. This interaction is particularly important for the establishment of succulent plant species in arid environments. Farfán-Heredia [43] studied the rate of recovering of populations of the columnar cactus *Polaskia chichipe* in natural and agroforestry systems. She found that the value of λ in agroforestry systems was over one, indicating that the recovery of the populations of this species has good conditions in agroforestry systems, particularly because of the permanence of shrubs and trees providing facilitation to the establishment of new plants of this species populations.

But, nevertheless the goodness of these systems, some problems put in risk their permanence. We have documented, for instance, that the vegetation cover is progressively decreasing in agricultural plots. The main causes are related to the fragmentation of land property. The original communal and ejidal land (two forms of collective property) used by a farmer has to be fractioned to benefit his descendants, each one of them receiving less land than their father and they have to intensify their smaller plot. In addition, we detected that the governmental programme "Procampo" which is expected to enhance agricultural land use consider that the patches of vegetation inside the crop fields decrease the agricultural area and farmers are penalized because of the presence of such vegetation patches [41]. Identifying the social problems making difficult the maintenance of agroforestry systems would be necessary for constructing policies for stopping the degradation of these systems and to favour their recover.

Raising of Goats

In the Tehuacán Valley livestock, mainly goats has been present since the Colonial times becoming in the main productive and activity [44]. Baraza and Estrella [42] estimated that nearly 5000 households raise goats in the region, in some municipalities being pastoralists more than 50 % of the households. People may consume meat during festivities, but the principal role of livestock is as "money box", since they may sell animals when they require monetary resources [41, 45, 46].

Livestock is raised through the system of extensive free raising. Domestic animals consume a broad spectrum of weeds, shrubs and trees, most of them wild species, and the diet is complemented with maize stubble from agricultural fields, which has high economic value [41]. In total, nearly 884 plant species of the region are used as fodder [30]. In the forests of communities studied, we have recorded on average 149 ± 21 wild and weedy species used as fodder [45–47], mostly species of Poaceae, Cyperaceae and Fabaceae [32]. Wild and ruderal plants are main sources of fodder during the rainy season, whereas agroforestry systems are important during the dry season. In agroforestry systems, Asteraceae are among the most important resources providing fodder, and constitute agro-silvo-pastoril systems, which provide fodder and benefit from the livestock faeces.

Because of the nearly 500 years of free raising of livestock, this has been considered a significant factor of impact on ecosystems. They have caused transformations of plant natural populations and vegetation cover, as well as soil erosion [42]. Their effect is particularly important in relation to the reducing of shade of nurse plants necessary for establishing of numerous plant species, the direct consumption of succulent plants, as well as impact associated to footsteps by animals (both elimination of seedlings and soil compactation, see [32]). Cattle in addition like to consume the apical meristems of agaves therefore impeding the development of escapes and sexual reproduction [35].

Nevertheless, livestock not only have negative effects. It has been documented that domestic animals may be seed disperesers of numerous plant species [48]. In the Tehuacan Valley, Baraza and Valiente-Banuet [49] recorded the favourable effect in seed dispersal and germination of a number of endemic cactus species as well as nurse plants of regional important for maintenance and restoration of natural environments. It has been in addition documented that populations of some endangered species such as *Mammillaria pectinifera* are favoured by livestock [50], and that domestic animals may favour plant diversity in agroforestry systems [23]. The main challenge for sustainable management of livestock is in relation of the level of intensity that ensures a good balance between the negative and positive effects. Land tenure system, number of animals allowed to raise per household, strategies to broaden the foraging area and decreasing the effect on small areas, production of fodder and methods for conserving and improving their nutritious qualities, are all issues for sustainable pastoralist management. For all these purposes, the inventory of plant resources used as fodder is an important source of information for innovations.

Extraction of Forest Products

Traditional botanical and ecological knowledge is dynamic. Local practices and techniques are continually in construction according to changes in both nature and society. In some cases the rhythms of technical construction are adequate to the rhythm of occurrence of the problems that motive them, but in other cases the socioecological processes overpass the capacity of constructing new techniques. The latter situations generally lead to critical situations and even the collapse of a management system or the extinction of a resource. In this section we illustrate this kind of processes with the case of the mescal agave "papalometl" *Agave potatorum*.

Production of mescal in the region started approximately one century ago in communities of the region that are still producers. For long time the production of mescal was destined to local parties and religious ceremonies and “cofradías”. However from some decades to the present the mescal spirits have gained popularity in the Mexican and international markets, which has dramatically increased the demand of these beverages and enhanced their production. In Mexico, mescal spirits are produced with at least 53 species recorded hitherto [44], but only six of them are cultivated in some way. In other words, most species used in Mexico to produce mescal are extracted from forests. In the Tehuacán Valley mescal is produced with seven species [36], but the most economically important is that produced with *A. potatorum* (Fig. 8.6). This agave species is naturally distributed from the Tehuacán Valley to the Central Valleys of Oaxaca. However, in the Central Valleys of Oaxaca the species is almost extinct because it has been extracted to produce the famous high quality mescal called “tobalá”. Therefore, the Tehuacán Valley is currently the main reservoir of genetic diversity of this plant species and the area from which the recovery of populations in the Central Valleys of Oaxaca will be possible. Therefore, protecting the populations from the Tehuacán Valley is of high priority.

Fig. 8.6 *Agave potatorum* (**a**) aspect of an individual just before producing the escape, the state in which it is used for producing mescal, (**b**) form of extracting and preparing de agave before cooking them in underground ovens, (**c**) aspect of a traditional distillery where mescal is currently produced

In order to develop criteria for use and conservation policies we have documented information about availability, traditional uses and management, reproductive biology, demography, biotic interactions and ecological processes required for establishment and population recovery of *A. potatorum*. Our general goal is to provide technical criteria useful for decision makers at the community and the Biosphere Reserve levels in order to prevent losing and favouring recovering of this important plant species. Delgado-Lemus et al. [36] characterized the process of mescal production, the extraction of agaves from forests, as well as the details of commercialization and interchange. An important aspect of that study was to estimate the amount of agaves available in a territory and the annual extraction rates, to have a figure of the magnitude of the problem. Summarizing, our information indicates that in the territory of a mescal producer village is nearly 10,000 adult individual plants available per year. Adult plants of agave are the only ones used for mescal production, and these are collected just before producing their inflorescence since that is the stage in which the stem has the highest content of sugar. Therefore, mescal production avoids sexual reproduction of the agave plants used. This is in general a problem since the extraction pattern may cancel the only reproductive mechanism, as it is the case of *A. potatorum*. In other agave species that combine sexual and vegetative propagation the problem associated of harvesting adult plants before sexual reproduction is reduction of genetic variation in populations. In the territory studied people harvest annually nearly 60 % of all the reproductive individual plants of *Agave potatorum* for mescal production. In fact, the amount harvested in this territory is insufficient for the mescal production (local mescal producers need nearly 12,000 agaves per year, 6000 are collected in their territory and the rest are bought to neighbouring villages). This is a number that allows visualizing a high impact on populations. But the impact may be even higher since agave harvest is not homogeneous in the whole territory, and some populations are drastically affected (in some of them all the reproductive agaves are collected). At present it is possible to identify areas where *A. potatorum* is extinct and local people affirm that it was present some 10–20 years ago.

Torres et al. [35, 51] conducted a demographic study in conserved populations in order to estimate the population growth rate (λ) and based on matrix analyses estimating limits for sustainable harvest, identifying the most vulnerable stages of the life cycle of the species and even simulating the optimum effort for recovering populations. All these studies were done with the purpose of generating recommendations to the local authorities of the community for a sustainable use of the agave populations. Collaterally, authorities and mescal producers from Tehuacán went to a workshop of interchange of experiences with the organization Sansekan Tinemi and the NGO Grupo de Estudios Ambientales, in the neighbouring region Montaña de Guerrero, which have developed important experiences for sustainable management of *Agave cupreata* which is phylogenetically close to *A. potatorum* and share similar biological and ecological problems for its management.

The results of demographic analyses indicated that even sites with relatively conserved populations are in risk. The study indicated that without any assistance this population will go to extinction in nearly 30 years (Fig. 8.7). Therefore, the estimation of any recommendation of sustainable harvest was impossible. However, the demographic models allowed important suggestion to optimize the actions for recovering populations. These identified that the most vulnerable stages for recovering populations are the juvenile stages 1–2 years old. The recruitment of plants of these stages of course requires the existence of reproductive individuals producing seeds and, particularly important, secure sites for their establishment.

Our studies identified two important problems associated to ensure these latter conditions. The first one is that the study by Estrella-Ruíz [52] documented that bats that pollinate *A. potatorum* decrease significantly their visits to plants in populations where the reproductive agave plants are scarce, because the offer of nectar and pollen is also low. Therefore, independently of numbers from matrix analyses, we know that adult plants require being abundant in order to ensure their reproductive success associated to their pollinator visits. We have not estimated a precise threshold in this respect and it is probably difficult to calculate it with certainty. We a priori estimated that 30–50 % of reproductive individual plants of agave should be respected in order to have high probability of reproductive success. The second problem was identified by Rangel-Landa et al. [53] and Torres

Fig. 8.7 General results of ethnobotanical and ecological studies on *Agave potatorum* and recommendations for more sustainable forms of management. (**a**) The general scheme of the life cycle indicating the probability of transition between life cycle stages, the probability of permanence, and the fecundity rate in two populations studied in the site "Xochitepec", $\lambda = 1.021$) (**b**) in the site "Machiche" $\lambda = 0.99$. (**c**) Aspect of facilitation interaction between a nurse plant species and *A. potatorum*. (**d**) Aspect of monitoring actions for improving management techniques for assisted recovering of *A. potatorum*. (**e**) Aspect of the communitarian nursery for producing young plants of *A. potatorum*

et al. [35, 51], who found that seeds and seedlings of *A. potatorum* require secure sites for germinating and surviving. In fact, we found that only 7–8 % of seeds arriving to secure sites germinates and very few seedlings survive after the first year. This situation shows a dramatic panorama of challenges for conservation and recovering of *A. potatorum* populations. However, our studies also revealed that in the laboratory it is possible to obtain 90 % of seed germination. In fact, people of the village started a project of producing agave plants in a communitarian nursery. But when they transplanted the young plants to the target area they obtained nearly 90 % of mortality of plants after 1 year. The reason: they mostly planted young plants in open areas. We then identified that *A. potatorum* seeds and seedlings require nurse plants for their establishment and that, in addition, the association is specific to some particular shrubby and small tree species. Through careful sampling of vegetation we have identified a list of plant species that are good nurse plants beneath whose canopies the young plants produced in the communitarian nursery should be transplanted to increase their survival probability. Finally, the local initiatives, the support by the authorities from the community and the Biosphere, the interchange of experiences with other successful communities and research conducted by our group have all contributed to construct technical proposals to attend a problem. Unfortunately, the problem of mescal production is not only technological, there is a complex problem associated to the unfair commercialization and that requires the intervention of other sectors interested in enhancing initiatives for sustainable management of plant resources and biodiversity conservation.

Throughout the experience commented and other similar related to other plant resources. Our research team has visualized the particular relevance of developing methods of participatory monitoring and systematization of actions. Local people are continually experimenting management techniques, looking for protection, conservation and recovering of their resources that are their own patrimony. Time is an important factor, sometimes actions start too late and their results are more probably unsuccessful. Rapid methods for learning the lessons from actions are particularly important. Interactions between sectors complementing the activities according to the responsibilities each one has to accomplish increase the complexity of actions but also the probability of success.

This is only one experience, but there are dozens of resources and ecosystems in risk. Our team has identified some of the plant species that require research and actions from different sectors of the Mexican society in the Tehuacán Valley. In Table 8.3 we include a list of the plant species that as *A. potatorum* and risk signs indicating that they require similar research efforts and actions. Ethnobotanical research and diagnoses of ecological and cultural status of plant resources have all been important windows to visualize important socioecological problems.

Table 8.3 The plant resources under the highest risk because of their ecological condition and the use intensity in the Tehuacán Valley

Use	Species
Edible plants	*Echinocactus platyacanthus*
	Clinopodium mexicanum
	Pachycereus weberi
	Dasylirion serratifolium
	Ceiba aesculifolia
	Neobuxbaumia tetetzo
	Lippia graveolens
	Litsea glaucesens
	Litsea neesiana
	Jatropha neopauciflora
	Agave potatorum
Medicinal plants	*Sellaginella lepidophylla*
	Juliana adstringens
	Euphorbia roseana
	Calea ternifolia
	Salvia oaxacana
	Satureja oaxacana
	Turnera diffusa
	Pittocaulon praecox
Ornamental plants	*Laelia albida*
	Dioon caputoi
	Echinocactus platyacanthus
	Mammillaria spp.
	Ferocactus spp.
	Fouquieria purpusi
	Beaucarnea gracilis
	Beaucarnea purpusi
	Agave marmorata
Fuel wood	*Prosopis laevigata*
	Parkinsona praecox
	Ipomoea arborescens
	Bursera spp.
	Acacia acatlensis
	Quercus spp.
	Lysiloma acapulcensis
	Taxodium mucronatum
	Juniperus spp.
	Pinus spp.
Handcrafts	*Brahea dulcis*
	Brahea nitida
	Dasylirion serratifolia
	Yucca periculosa
	Bursera glabrifolia
Beverages	*Agave potatorum*
	Agave marmorata
	Agave titanota
	Agave salmiana var. ferox

Based on information about distribution, abundance, cultural value (Casas et al. [32]) and interchange in markets (Arellanes et al. [34])

Fuel Wood Extraction

The Tehuacán Valley has been recognized as a zone critical for analysing solutions of problems related to bioenergetics resources, since fuel wood if already highly used and it is predictable an increasing use of a number of well-identified species [54] that require special protection and designing sustainable management strategies. In six communities we documented in detail the consumption of plant resources

Table 8.4 Firewood consumption and plant species mostly used in villages of the Tehuacán Valley

Village	Species	Annual consumption (Ton)	Annual consumption (%)
Nodón	*Juniperus flaccida*	79.94	33.33
	Quercus peduncularis	26.64	11.11
	Quercus candicans	–	–
Total/village	15	239.8	100
Atolotitlán	*Dodonea viscosa*	222.88	33.33
	Acacia acatlensis	167.18	25
	Montanoa sp.	55.70	8.33
	Quercus spp.	55.70	8.33
Total/village	29	669	100
Ixcatlán	*Quercus liebmannii*	1001.44	75.95
	Quercus urbanii	93.7	10.48
	Quercus castanea/*Quercus obtusata*	22.24	1.67
Total/village	23	1282.5	100
San Lorenzo Pápalo	*Quercus conzatii*	718.68	57.6
	Quercus magnolifolia	420.321	34.74
	Quercus glaucoides	91.46	3.02
	Quercus peduncularis	23.52	1.9
	Pinus spp.	20.90	1.72
	Lysiloma acapulsensis	7.84	0.64
Total/village	41	1206.07	100
Quiotepec	*Acacia cochliacantha*	121.71	26.23
	Pinus sp./*Quercus* sp.	103.1	22.21
	Prosopis laevigata	51.55	11.11
	Leucaena leucocephala	51.55	11.11
	Escontria chiotilla	26.12	5.62
Total/village	67	464	100
Zapotitlán	*Mimosa luisana*	80.49	38.18
	Prosopis laevigata	37.21	17.65
	Acacia constricta	29.72	14.1
	Myrtillocactus geometrizans	28.6	13.57
	Stenocereus stellatus	12.71	6.03
Total/village	25	210.83	100

used as fuel wood [33, 45–47, 55]. We found that all households make use of fuel wood for cooking food, boiling water and heating homes, even when use of gas stoves has increased. For instance, in Santa María Ixcatlán gas stoves increased from 15 % of households by the year 2000 [45] to 35 % by 2012, but only 30 % of these households make a daily use of their stoves, 30 % occasionally, and 40 % almost never use their gas stoves since it is difficult and expensive to obtain provision of gas. The average consumption of fuel wood for domestic issues in all localities studied is 678.62 ± 191.43 (X ± SD, $n = 6$ villages) tons per year per community (Table 8.4) [32], obtained mainly from 209 species belonging to the families Mimosaceae, Fagaceae, Asteraceae, Cactaceae and Burseraceae [30].

Fuel wood is in addition used for other productive activities such as artisanal manufacturing of bread in all the localities studied, the manufacturing of bricks and tiles, particularly important in the community of Ajalpan, as well as the production of pottery, particularly important in Los Reyes Metzontla, and the mescal production in at least seven communities of the region.

In relation to theses productive activities, fuel wood is provided by a more reduced or specialized group of species. For instance, for manufacturing pottery people of Metzontla do not make use of ovens but the ceramic is fired. They have to utilize species with specific heat, carefully selected in order to achieve the appropriate baking point. The commonly use Wood of *Lippia graveolens*, *Acacia* spp. and *Lysiloma acapulcensis* for establishing a basis or “bed” where the ceramic is settled, and then wood with lower calorific capacity such as *Ipomoea arborescens* and *Agave* spp. leaves which cover the pottery pieces. For manufacturing bricks and tiles is commonly used *Viguiera dentata*, an annual Asteraceae producing woody stems very much appreciated for this productive activity. For producing mescal, people make use of wood of particular tree species; for instance, in San Luis Atolotitlán people use 15–20 kg of wood of “pirul” *Schinus molle* for producing 1 L of mescal, whereas in Santa María Ixcatlán people use 13–18 kg (36 al 40 % are *Quercus laeta*, *Q. liebmanni* and *Q. urbanii* and the remaining is provided by eight oak species, *Arbutus xalapensis*, and *Juniperus flaccida* [45, 56]).

Commercialization of fuel wood is allowed by local authorities among persons of a village; this fact is normally based on local agreements and norms, particularly for those people with difficulties for obtaining the fuel wood (e.g. old people), taking care of the local and regional agreements to collect fuel wood from dead wood. The regional commercialization of fuel wood is prohibited and considered by the regional authorities regulating environmental issues as incompatible with conservation goals [57]. However, the high demand of fuel wood in regional cities and suburban areas motivates illegal commercialization of fuel wood (mainly of oak and pine species and the mesquite *Prosopis laevigata*) in the main regional markets [34]. The main sources of fuel wood to the regional markets are the highlands neighbouring to the markets, particularly the Sierra Negra, the Sierra Mazateca and Coixtlahuaca [57].

Extraction of fuel wood involving taming of trees and shrubs, together with the impact of overexploitation of forest by livestock raising may endanger the conservation of a broad spectrum of species, not only those directly used. In the village of

San Lorenzo Pápalo we estimated that the community would require nearly 1.3 ha of forest per year to satisfy the demand of fuel wood which is approximately 21,619 m^3 of wood, which is provided nearly 60 % by the species *Quercus conzatii* [46]. This scenario may occur similarly in several communities, but in counterpart the communities commonly have collective regulations that for long time have protected trees and forests. Although fuel wood is obtained mainly in forests from common property areas, where all members of a community have the right to make use of the collective resources, a considerable proportion of plant resources is obtained from agroforestry systems, where trees and shrubs are let standing and maintained as described above. Among the principal motives why people maintain woody plants in these systems is provision of fuel wood [23, 25, 26].

In addition to the local Regulations, there are valuable initiatives from governmental, non-governmental and academic institutions in promoting more efficient forms of consuming fuel wood, particularly through efficient stoves. Particularly active have been programmes from the authorities of the Biosphere Reserve, the UNAM, and some regional NGOs. But these initiatives not always have been successful neither sufficient. A review of the experiences in this and other regions is necessary for designing more efficient strategies of vinculation and adoption of technological innovations in this direction. In addition, some communities and local authorities have had the initiative of recovering populations of particularly valuable species used as fuel wood. These are the cases of *Lysiloma acapulcense* and *Acacia* spp. in San Luis Atolotitlán and Caltepec, as well as *Ipomoea arborescens* in Los Reyes Metzontla. But undoubtedly these two routes of attending the problem, as well as others still poorly explored (alternative renewable energies) require more systematic initiatives, more research, technological innovation, and construction of collective agreements and norms in order to protect the most affected species illustrated in Tables 8.3 and 8.4. Systematic monitoring of amounts of fuel wood consumption, the species studied, patterns of wood extraction, recovering of critical species, regulation of fuel wood commerce are all critical actions necessary for the ordination and sustainable use of fuel wood providing species at regional level.

Final Comments

The traditional systems of plant and ecosystems management are not static, they are in continual innovation and construction. There is a valuable reservoir of techniques associated to traditional ecological knowledge that deserves attention of academic and non-academic sectors of the society. Time is one of the main challenges for sustainable management and the local experiences constitute a form to shorten the way of constructing technological strategies with a social and cultural basis adequate to local ecosystems and resources. Promoting the interchange of local traditional knowledge and management experiences is a process that would make possible to increase the potentialities of this important tool. In addition, scientific research may be an important ally; academics have the possibility (and possibly the duty) of developing studies in order to reinforce and improve such processes of technological innovation. Ethnobotanists, ecologists, economists and social scientists have many things to do together with local communities and other sectors of the society for constructing sustainable management strategies.

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Chapter 9
Domestication of Plants in Mesoamerica: An Archaeological Review with Some Ethnobotanical Interpretations

Barbara Pickersgill

Abstract The great pre-Columbian civilisations of Mesoamerica depended on domesticated plants, notably maize, beans, squashes, grain amaranths and fruits, including avocado, together with cotton for fibre. Domestication is difficult to define in a way that fits this diversity of species and range of human exploitation. Different species were domesticated in the semi-arid highlands and the humid lowlands, but the archaeobotanical record is still frustratingly fragmentary and does not include the transition from wild to domesticated for any species. In the highlands, cultivation seems to have started with *Lagenaria, Cucurbita, Agave* and *Opuntia* in the semi-arid valleys, and possibly maize and grain amaranths around lake margins. In the lowlands, most early records of domesticated plants require confirmation. Maize spread relatively rapidly after its domestication, but only as a minor component of the diet. Beans appear at approximately the same time as pottery, possibly because long boiling in fireproof containers was then possible. Manioc was introduced from South America and became a staple among the Classic Maya. Residues in potsherds show that a chocolate drink was made by the Olmec and their successors, but may have been made from an indigenous species of *Theobroma*. However South American *T. cacao* was undoubtedly present by Maya times. Plant domestication in Mesoamerica thus began slowly, with more species added gradually to the list of domesticates, but by the time of the Spanish Conquest pre-Columbian farmers had developed an impressive array of different types of maize, beans, chile peppers and other crops.

Keywords Domestication • Archaeobotany • Maize • Beans • Squash • Grain amaranths • Cotton • Chocolate • Olmec • Maya

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Fig. 9.1 Map of Mesoamerica

Mesoamerica, as defined by archaeologists and shown in Fig. 9.1, extends from central Mexico south to the Pacific slopes of Nicaragua and Costa Rica [1]. This is the region in which many of the great civilisations of the Americas developed: the Olmec, followed by the Maya, the inhabitants of Teotihuacán, and the Zapotec, Toltec and Aztec. All were, to a greater or lesser extent, dependent on agriculture and, since pre-European Mesoamerica had only two domesticated animals, turkey and dog, were therefore dependent, partially or completely, on domesticated plants.

Mesoamerica has long been recognised as one of the major regions of the world in which plants were domesticated [2]. Species domesticated here include a major cereal (maize, *Zea mays*), a major pulse (common bean, *Phaseolus vulgaris*), a major spice (chili pepper, *Capsicum annuum*), and a major fibre (upland cotton, *Gossypium hirsutum*), as well as various vegetables, including squash (*Cucurbita* spp.) and probably tomato (*Solanum lycopersicum*), together with a variety of fruits, of which avocado (*Persea americana*) is perhaps the best-known. Some other species that are not economically important today were nevertheless extremely significant in pre-European times, notably the grain amaranths (*Amaranthus hypochondriacus* and *A. cruentus*), which ranked only a little behind maize and beans in the lists of tribute exacted by the Aztec Empire [3]. Casas et al. [4] estimated that Mesoamericans domesticated or are domesticating over 200 native species and currently utilise between 5000 and 7000 plant species.

Domestication and Its Recognition

Charles Darwin never found it necessary to define domestication in his two volumes on “The Variation of Animals and Plants under Domestication” [5]. Since then, ethnobotanical and other studies have shown that human interactions with plants involve a continuum from simple exploitation of wild populations, through various degrees of management of populations still growing in the wild, to cultivation and ultimately to plants becoming dependent on humans for successful propagation. This continuum has created problems in producing a universally applicable definition of domestication. A generally accepted starting point is that domestication results in genetic changes in the features of the organism (i.e. its phenotype) in response to selection in environments created or modified by humans. These changes in phenotype make up the domestication syndrome. When they involve morphological characters, it may be possible to identify archaeobotanical specimens as coming from domesticated, as opposed to wild, individuals. Loss of mechanisms for fruit or seed dispersal is often cited as the most common trait of the domestication syndrome, and is frequently recognisable archaeologically. However, when all categories of crops, not just annual seed crops, are considered, change in secondary metabolites, affecting characters such as flavour, toxicity or colour, is the trait most frequently altered by domestication [6]. For most crops, it is not yet possible to monitor change in secondary metabolites in archaeobotanical specimens, so this sign of domestication may go undetected.

Domestication is now recognised as an evolutionary process. Evolution is an attribute of populations, not individuals, so this has led to definitions of domestication that similarly emphasise populations rather than individuals. Clement [7] defined domestication as a process causing genetic changes in populations such that the average phenotype diverges from the range found in wild populations, while Fuller [8] defined a domesticated population as one containing a statistically significant majority of domesticated as opposed to wild phenotypes. These definitions may cause difficulty in the archaeological recognition of domestication, since they either imply or explicitly state that some individuals in a domesticated population will have the wild phenotype for one or more characters. Archaeobotanical specimens may not be recovered in sufficient numbers to constitute the statistically significant sample required by Fuller’s definition, or may come from contexts likely to represent a skewed sample. For example, a midden may contain predominantly specimens rejected by human selection, in which the wild phenotype is thus likely to predominate, whereas storage vessels may contain predominantly specimens favoured by human selection, in which the domesticated phenotype is likely to predominate.

To accommodate intermediate stages along the continuum from wild to domesticated, Clement [7] proposed the categories of incipient domestication and semi-domestication. An incipiently domesticated population has been modified by human selection and intervention, but the average phenotype is still within the range found in wild populations for the trait(s) under selection. A semi-domesticated population has been significantly modified by human selection and intervention, so that the average phenotype may diverge from the range found in wild populations for the trait(s) under selection. Study of the interactions of people with plants that today are at only the stages of incipient domestication or semi-domestication may lead to a better understanding of the processes leading to domestication in prehistory [4]. In this chapter, a broad definition of domestication is adopted, including both incipiently domesticated and semi-domesticated species.

Ecological Background to Plant Domestication in Mesoamerica

The number of species that have been partly or fully domesticated in Mesoamerica reflects the richness of the flora, which in turn reflects the diversity of the terrain. In the northern part of the region, the high plateau of the Mesa Central is bounded to the west and east by mountain chains that parallel the Pacific and Atlantic coasts, and bounded to the south by the Trans-Mexican Volcanic Axis, which contains the highest and most active volcanoes in Mexico. The Aztecs and, before them, the inhabitants of Teotihuacán, had their major cities on the Mesa Central. The Trans-Mexican Volcanic Axis separates the Mesa Central from the Mesa del Sur, occupied by the Zapotec and Mixtec peoples and separated by another mountain barrier from the Gulf Coast lowlands of the present-day Mexican states of Veracruz and Tabasco. These were the heartland of the Olmec civilisation. The Isthmus of Tehuantepec, which is just 200 km wide, with an altitude at the Continental Divide of only about 250 m, provides a corridor between the Gulf and Pacific lowlands. The highlands continue south of the isthmus through the Mexican state of Chiapas to Guatemala and Honduras. This region was the centre of the highland Maya. The lowland Maya were centred on the Yucatán peninsula, a large shelf of extremely porous limestone projecting into the Gulf of Mexico.

The climate of Mesoamerica is seasonal, though the length and severity of the dry season vary. The lowlands of the Gulf Coast have only a short dry season and their natural vegetation is a species-rich tropical humid forest. The lowlands of the Pacific coast receive less rain, have a longer dry season and their natural vegetation is semi-deciduous or deciduous forest, with scrub or grassland in the drier areas. In the highlands, the eastern edge of the Mesa Central is in the rain shadow of the Sierra Madre Oriental and its natural vegetation is semi-desert scrub with thorny legumes and cacti. This scrub continues along the southern edge of the plateau, through the Tehuacán valley into the Oaxaca basin. The central and western parts of the Mesa Central and the surrounding mountains receive more rain and were originally covered by pine-oak forests. These forests continue south through the highlands of northern Central America to the southern limit of Mesoamerica.

There is therefore a marked dichotomy between the humid lowlands, where plant growth is possible virtually year-round, and the semi-arid regions where plant growth is seasonally restricted by low temperatures (in the highlands) and/or lack of moisture (in the highlands and some parts of the lowlands). This dichotomy is reflected in the crops domesticated in the two regions. In the semi-arid zones, agriculture is based on annual species such as maize, beans and squash, grown for and/

or propagated by seeds. In the humid lowlands, root crops and perennial fruit trees assume greater importance, though seed crops, notably maize and beans, were and are also of considerable significance. There is a long-standing controversy about the primacy of the lowlands versus the highlands, and hence root crops versus seed crops, in the origins of agriculture (see, e.g. [9, 10] vs. [11]).

The Sequence of Plant Domestication in Mesoamerica

The archaeobotanical record in Mesoamerica is still frustratingly fragmentary. As McClung de Tapia [12] commented, these deficiencies are sometimes due to inadequate preservation, especially in the humid lowlands and in open sites, but sometimes due to excavation of the wrong sites, or the wrong parts of the right sites. This occurs when studies of subsistence were not the main goals of the excavators. Specimens illustrating transitions from wild to domesticated phenotypes are generally lacking, so it is usually not possible to determine for any given crop in what order different traits of the domestication syndrome arose, and hence what priorities may have driven selection in early cultivated or manipulated populations.

The relatively recent discipline of palaeobiolinguistics provides data independent of archaeology on when, and in some cases where, certain species became important to humans. By comparing core vocabularies in languages that have diverged from a common ancestral language, and by assuming that these core vocabularies diverged at a constant rate, the number of centuries that have elapsed since these languages diverged can be estimated [13]. Words in related languages

Fig. 9.2 Major archaeological sites mentioned in the text

that are descended from a common ancestral word and thus resemble one another in form and meaning can be used to reconstruct a hypothetical proto-word and to suggest items that were known to speakers of the proto-language. All the basic assumptions of palaeobiolinguistics have been severely criticised, but it remains the only existing method for relating results from linguistics to results from archaeology [13]. As a complement to archaeobotanical data, palaeobiolinguistic data, where available, are therefore included in this review.

The locations of important archaeological sites mentioned in the text are shown in Fig. 9.2.

The Archaic Period and the Beginnings of Plant Cultivation, Before 4500 BP

The earliest specimens of domesticated plants so far recovered in Mesoamerica are squash (*Cucurbita pepo* ssp. *pepo*) and bottle gourd (*Lagenaria siceraria*), from two sites in the highlands: Guilá Naquitz cave in the Valley of Oaxaca and Coxcatlán cave in the Tehuacán Valley. The specimens from Guilá Naquitz have been directly dated to about 9900 calendar years before the present (cal.BP) [14] and those from Tehuacán to about 7900 cal.BP [15]. At that time, the caves were apparently used by small groups of nomadic hunter-gatherers. Bottle gourd is not known in the wild anywhere in the Americas, so presumably reached the highlands as a species that was already domesticated, or at least cultivated. Its dried fruits were probably valued as liquid-proof containers by peoples who lacked pottery. *Cucurbita pepo* ssp. *pepo* also has no known wild ancestor. Some of the seeds from Guilá Naquitz, including one that was directly dated, were larger than those of any known wild species of *Cucurbita* so were considered to be from a species that was already domesticated [16]. Small *Cucurbita* seeds present in the same levels as the large seeds were thought by Whitaker and Cutler [17] to be “perhaps of a wild progenitor of the cultivated species”. These small seeds have still not been satisfactorily identified. Brown [18] reconstructed a name for squash in the earliest Mesoamerican proto-language, Proto-Otomanguean, which is considered to be a highland language that originated in north-west Oaxaca, and which Brown dated to 6591 BP. The next-oldest proto-language in which Brown could reconstruct a term for squash was Proto-Mayan, dated about 2220 BP. Brown therefore suggested that the speakers of Proto-Otomanguean may have been the people responsible for the domestication of *C. pepo* in Mesoamerica. This was probably for its edible oil-rich seeds, since the fruits were unlikely to be eaten until human selection had eliminated the bitter flesh characteristic of wild *Cucurbita*. Increased seed size apparently preceded increased fruit size by about 1000 years [16], which also suggests that seed, not fruit, was the first target of human selection. Both bottle gourd and squash are fast-growing herbs that, if sown on cleared or otherwise disturbed ground, will out-compete most other colonising species. They are therefore suitable for cultivators with a nomadic lifestyle.

Brown [19] also reconstructed names in Proto-Otomanguean for maguey (*Agave*), nopal (*Opuntia*), avocado and maize, so concluded that all these were important to highland people by at least 7000 BP. The archaeological record supports his conclusions for maguey, nopal and avocado, but maize is more controversial. The fleshy leaves of maguey may be roasted and chewed until only a quid of fibrous tissue remains and is discarded. Such quids were present in all levels of the Tehuacán caves [20] and Guilá Naquitz [21], and also from Archaic levels onwards in the rock shelter of El Gigante in highland Honduras, where only the leaves seem to have been roasted in Archaic times, while the more labour-intensive practice of pit-roasting the entire head commenced only in the late Formative [22].

Opuntia was likewise an important element in Archaic subsistence. The flattened stem joints (cladodes) are today cooked as a vegetable, the fruits are eaten raw or processed, while the seeds may be roasted, ground and used in sauces [23]. Fragments of cladodes, fruits and seeds were recovered from early levels of both Guilá Naquitz and the Tehuacán caves [20, 21] and were also identified in Archaic coprolites from the Tehuacán caves [24]. Earle Smith, botanist to the Tehuacán project, wrote that "in spite of lack of evidence to prove it, I am convinced that nopal and maguey are the earliest cultivated plants of the Tehuacán region" [20]. On the other hand, MacNeish, leader of the project, wrote "I see little or no evidence of the cultivation of maguey [or] *Opuntia* … nor do I see any evidence that these were among the first domesticates which led to the domestication of such plants as corn, beans and squash" [25]. Both *Opuntia* and *Agave* occur in the natural vegetation around Guilá Naquitz and the Tehuacán caves. Both are easy to propagate vegetatively and need little attention thereafter so, like squash and bottle gourd, could be cultivated successfully by semi-nomadic people. Both have been minimally affected by human selection despite their long-continued use by humans, so qualify only as incipient domesticates.

Avocado seeds were present in the Tehuacán valley caves from about 7000 BP. Even the oldest were very similar in size to seeds from fruits purchased in the local market [26]. From about 6500 BP the climate of the Tehuacán valley was apparently too dry to support wild avocado, so the trees were probably cultivated near the river or where the water table was reasonably accessible [20, 27]. Other tree species with edible fruits that were present in Archaic levels of the Tehuacán caves but do not occur wild in the valley today include hog plum (*Spondias*), black sapote (*Diospyros digyna*), white sapote (*Casimiroa edulis*) and coyol palm (*Acrocomia aculeata*). Smith [20] considered that all were introduced to the valley as species first taken into cultivation elsewhere and required some form of water management to be grown successfully in the Tehuacán valley, whereas Buckler et al. [27] argued that some or all could have grown wild in the valley in wetter periods in the past. These species may have been tended or even cultivated to maintain or enhance their numbers when the climate deteriorated, but have not moved beyond the categories of incipient or semi-domesticates.

Brown [19] considered, on palaeobiolinguistic grounds, that maize was important to highland people by 7000 BP. Cobs from the Tehuacán caves were originally claimed to date back to about 7600 BP and to represent wild maize [28]. Direct dating subsequently showed that the oldest of these cobs dated to only about 4750 BP [29]. This revised date is generally accepted, though not by all [30]. The earliest macrobotanical remains of maize are now considered to be four small cobs from Guilá Naquitz cave, directly dated to about 6250 cal.BP [31]. These were regarded as domesticated because they had a tough rachis, i.e. had lost the mechanism for separating seeds from the cob, but were considered to represent an early stage in domestication because they showed a mixture of traits of domesticated maize and its presumed wild ancestor teosinte [32]. The early Tehuacán cobs have likewise been examined by many different authorities and the general consensus is that they too represent domesticated, not wild, maize [33].

MacNeish [25] suggested that chile pepper and amaranth were also among the crops domesticated in the Tehuacán valley. Most of the early specimens of chile pepper that I have seen are seeds and are within the size range of modern wild *Capsicum annuum*, while the single fruit from Archaic levels was also very similar to modern wild *C. annuum* (Pickersgill this volume). The large fruit fragment considered by Smith [20] to be indistinguishable from local domesticated chile was not available for study and does not fit with the sizes of the seeds from Archaic levels. Wild *C. annuum* does not occur in the Tehuacán valley today, but its fruits are easily dried and the dry fruits are light, easily transportable and retain their pungency, so were probably an attractive trade item. The question of when and where *C. annuum* was domesticated remains open.

Domesticated amaranths have pale seeds, rather than the dark seeds of their wild relatives. Two species, *Amaranthus cruentus* and *A. hypochondriacus*, were domesticated in Mesoamerica and both have been identified from the Tehuacán caves; *A. cruentus* at about 6000 BP, *A. hypochondriacus* at about 500 BP [34]. Neither species is known in the wild and opinions on their ancestry differ. The wild species *A. hybridus* is certainly implicated and may be the sole ancestor of *A. cruentus*, while *A. hypochondriacus* may have been domesticated in a different area from a distinct population of *A. hybridus* [35], or may have originated from a different, as yet unidentified, wild species [36, 37]. *Amaranthus hybridus* is a common weed of arable crops, and is gathered as a quelite or edible leaf vegetable. In the Tehuacán valley today, it is one of the species left for future use when cultivated plots are weeded and its density is enhanced by encouraging seed dispersal [38]. This is a scenario that Casas et al. [4] considered could lead to domestication. As a plant adapted to disturbed areas, amaranth, like bottle gourd and squash, could be grown by semi-nomadic peoples and could produce a crop of edible leaves or seeds with little need for weeding, fertilising or irrigating.

An alternative setting to semi-arid valleys for the beginning of plant cultivation in the highlands is lake margins, where fish, waterfowl and other aquatic resources would be available year-round; fertile alluvial soils would permit good growth of useful wild, and subsequently cultivated, plants; and surrounding forests would provide opportunities for hunting and for gathering of fruits and nuts in season. All this would permit development of the sedentary lifestyle required if agriculture is to become a major means of subsistence. Unfortunately few lake margin sites have been investigated and even fewer fully reported. Excavations at the edge of Laguna

Tuxpan in the central Balsas basin of western Mexico produced phytoliths identified as derived from cobs of maize and rinds of squash and minimally dated to 6000 cal.BP, suggesting that both species were cultivated on soils exposed as the lake shrank in the dry season [39, 40]. The squash phytoliths were identified as from domesticated plants because of their size, and as *Cucurbita argyrosperma* because today wild populations of this species occur only 45 km away [39]. However, recent data suggest caution in using phytolith size as a criterion for recognising domestication until more is known about effects of environmental variables such as moisture availability and disease infection [40]. Phytoliths and starch grains identified as those of maize, not teosinte, were recovered from stone tools from a nearby rock shelter as well as from soil samples. Some of these tools came from levels below those dated 8990–8610 cal.BP [41]. It has been suggested that the first use of *Zea* (initially teosinte, later maize) by humans was for the sweet stalks, which could be chewed like sugar cane, or used to produce syrup, sugar or, after fermentation, beer [42, 43]. However, phytoliths characteristic of stalks, not cobs, of *Zea* were absent from both grinding stones and associated sediments, so Piperno et al. [44] concluded that maize was first grown for its grain, not for sugar in the stalks. The data from the Balsas basin bring the archaeological record of maize closer to the time of divergence of maize from teosinte (i.e. the time of domestication of maize), estimated from molecular data at 9188 BP [45], and the suggestion from linguistic data that maize was important to highland peoples by at least 7000 BP [19]. However, both molecular and linguistic estimates involve assumptions that may prove unjustified, while microbotanical data (pollen, phytoliths, starch grains) are often controversial because of uncertainties in identification and/or limited sample size and/or post-depositional movement. Directly dated macrobotanical specimens antedating the early cobs from Guilá Naquitz cave are still needed to resolve questions of where, when, how and why maize was domesticated.

At the site of Zohapilco, on the shore of the southern part of the lake system in the Basin of Mexico, excavations suggested that the inhabitants were fully sedentary some three millennia earlier than the inhabitants of the Tehuacán valley [46]. Pollen studies showed that from about 8000 to 6500 BP much of the basin was covered by pine, oak and alder forest, but around the lake herbaceous plants included *Amaranthus* or *Chenopodium* and *Zea* (presumably teosinte). Seeds recovered from hearth areas included *Amaranthus* and one seed of *Cucurbita*, while macroscopic remains from other parts of the site included a few grains of teosinte, seeds of *Physalis* (the genus that includes the Mexican green tomato as well as some purely wild species), and chayote (*Sechium edule*). Chayote is a cucurbit with a large edible tuberous root, young shoots and leaves that can be cooked like spinach and a fruit that is bitter in wild species but non-bitter in the domesticate. It is not clear whether the species reported archaeologically from Zohapilco were domesticated, cultivated or merely exploited, but Niederberger [46] considered that in the Basin of Mexico experimentation with agriculture probably began 7000–8000 years ago.

Relatively few Archaic sites are known from the tropical lowlands. Macrobotanical specimens are rarely recovered, so deductions are made instead from the pollen and phytolith record. Pollen grains and phytoliths are not usually directly dated, and Blake [47] advised caution over accepting indirect dates from associated charcoal.

Much attention, and controversy, has concerned the record of maize in the lowlands. It is now generally conceded that pollen of maize cannot be reliably distinguished from pollen of teosinte. Furthermore, teosinte was more widespread in the past than it is now. Wilkes [48] graphically described how, in his professional lifetime, carpets of teosinte have been replaced by a patchy quilt of cattle pasture as land is cleared for farming. Relict populations of teosinte have recently been discovered in the Papaloapan river drainage in Oaxaca, in southern Mexico, and in southwest Nicaragua [49–51]. These newly found populations are not thought to be implicated in the origin of maize, but they do suggest that claims that prehistoric pollen grains of *Zea* represent domesticated maize simply because teosinte is not known today in the area concerned need to be supported by additional evidence.

At the site of San Andrés on the Gulf coast of Tabasco, located on a land barrier separating a freshwater lagoon from the sea, thus with access to both cultivable land and aquatic resources, a core showed that pollen of *Zea* appeared abruptly around 7100 cal.BP, along with charcoal and pollen of other grasses [52, 53], but this could reflect fire caused by lightning, not necessarily fire set by humans to clear land for cultivation. However, sediment samples from about 7300 cal.BP contained phytoliths common in maize but not in teosinte. Pohl et al. [53] claimed the San Andrés pollen grains and phytoliths as the earliest and best-documented evidence of maize in Mexico, 5800 years older than the earliest cobs from Guilá Naquitz cave in the highlands. The San Andrés microremains were not directly dated, so their age has been considered suspect [54], leaving the earliest securely dated specimens of maize as the cobs from Guilá Naquitz cave.

On the Pacific coastal plain, south of the Isthmus of Tehuantepec, in an ecological setting comparable to that of San Andrés, a core taken near Cerro de las Conchas, a shell mound occupied periodically from 7500 to 5500 cal.BP, showed that around 6500 cal.BP weedy grasses became dominant and maize cob and leaf phytoliths appeared [55]. Phytoliths of Podostemaceae, species of which grow in fresh water, were also frequent, so Kennett et al. [55] suggested that the whole phytolith assemblage had originated in agricultural fields away from the coast and been transported by flood waters to the mangrove swamps of the Acapetahua estuary. They therefore considered that, 6500 years ago, these Archaic people were practising slash-and-burn farming, supplemented by marsh clams and other estuarine resources.

Zea pollen has been reported in Archaic levels of cores from various other lowland sites: a freshwater lake in an estuarine setting on the Gulf coast of Veracruz at 4830–4530 BP [54]; a lake in western Honduras at about 4770 BP [56]; Cob Swamp in northern Belize about 4400 BP [57]; a lake in El Salvador at 4440 BP [58]. The cumulative effect of these reports led Blake [47] to suggest that maize planting expanded through Mesoamerica between 4700 and 4200 BP. Macroscopic remains are needed to remove lingering doubts about whether teosinte was present in any of these areas at these times, but so far the only macroscopic remains of maize from south of the Isthmus of Tehuantepec are from the El Gigante rock shelter in Honduras. These are only about 2200–2000 years old [22], thus significantly younger than the earliest cobs from Guilá Naquitz.

Cotton pollen has been reported from around 4300 BP in a core from San Andrés [52], but the Gulf coast of Tabasco is within the range of wild cotton and pollen grains provide no characters by which domesticated cotton can be distinguished from wild cotton. Cotton pollen has also been reported in the same levels as *Zea* pollen in a core taken near Cerro de las Conchas in the Acapetahua estuary on the Pacific coast [55]. This is outside the accepted range of wild, as opposed to feral, *Gossypium hirsutum*, but only a single pollen grain was found. It is quite likely that cotton was cultivated on the Pacific coast in Archaic times, but one pollen grain is very flimsy evidence on which to base this conclusion. Scraps of cotton fibre and fruit fragments were recovered from levels dated about 5500 to 4300 BP in caves in the Tehuacán valley. Some of the fruit fragments were originally stated to be similar in size to wild *G. hirsutum* [20], though the cotton was later considered to be already fully domesticated [59]. Wild *G. hirsutum* appears confined to the north coast of the Yucatán peninsula and, further north, the coast of Tamaulipas [60] and may have been domesticated twice; once in southern Mexico or Guatemala, giving rise to the commercially important Upland cottons, and once in northern Mexico, giving rise to the cotton grown by the Hopi of the southwestern United States [61]. Cotton was reported from the Ocampo caves in Tamaulipas from 3800 BP onwards [62], but the specimens do not seem to have been described in detail. The appearance of cotton in the Tehuacán caves suggests contact between the highlands and the lowlands in Archaic times, but the presence of fruit fragments as well as fibre suggests that it may have been grown in the valley after its introduction from the lowlands, because trade would probably involve seeds with their attached fibre, or fibre alone, rather than fruits.

Other reports of Archaic cultigens in the lowlands need confirmation from more extensive finds and/or macroscopic remains. Phytoliths of either *Cucurbita* or *Lagenaria* were reported in a core from the Pacific coast of Guatemala, at an age of about 4800 BP [63]. The same core yielded phytoliths of *Maranta* in a level dated about 4600 BP. However, wild species of *Maranta* occur in Central America, so this is not necessarily evidence for cultivation of arrowroot (*M. arundinacea*). Although species grown for their starch-rich underground storage organs are generally important in the lowland tropics, very little is known of the origins or antiquity of those that may have been domesticated in Mesoamerica. Bronson [64] listed sweet potato among only ten species with names common to all branches of the Maya language, so considered that it must have been known before 4000 BP and Brown [19] concluded, albeit tentatively, that sweet potato was familiar to and important among highland people by 3200 BP, but it has no archaeological record in Mesoamerica.

Lentz et al. [65] claimed that sunflower was domesticated in Mexico, independently of and earlier than its generally accepted domestication in eastern North America, on the basis of a carbonised kernel and achene found at San Andrés in lowland Tabasco and directly dated to about 4100 BP. Subsequently, Heiser [66] suggested that the specimens were probably bottle gourd seeds. Brown [19] was unable to reconstruct a name for sunflower in any of 30 ancestral Mesoamerican languages, so concluded that it was probably a very recent addition to the plant species exploited in Mesoamerica.

The Formative or Pre-Classic Period, About 4500–1750 BP

The invention or introduction of pottery marks the end of the Archaic and start of the Formative Period. Pottery expanded the range of cooking techniques available, since food could now be boiled in fireproof containers as well as being roasted or baked. It has been suggested that beans were domesticated only after acquisition of pottery allowed them to be boiled long enough to become edible [67]. In the Basin of Mexico, at the site of Terremote-Tlaltenco, quantities of carbonised and uncarbonised seeds of common bean (*Phaseolus vulgaris*) were recovered in pottery vessels associated with hearths, and also in baskets, in levels dated about 3400–3300 BP [68]. If this age is correct, these beans antedate directly dated common beans from Guilá Naquitz, the Tehuacán valley caves and the Ocampo caves in Tamaulipas, all of which proved to be much younger than previously thought, dating to only about 2300–1250 cal.BP [69]. The 7000 BP seeds from Guilá Naquitz originally reported as wild *P. vulgaris* were subsequently re-identified as a wild legume, possibly *Phaseolus,* but not any of the species later domesticated [69].

In the lowlands, beans (probably *P. vulgaris* but possibly also the tepary bean, *P. acutifolius*) and pottery also appeared apparently simultaneously in sites on the Pacific coast of southern Mexico and Guatemala. The earliest directly dated specimen (about 3400 cal.BP; Blake cited in [70]) is approximately contemporaneous with the early beans from the Basin of Mexico. Beebe et al. [71] and Chacón et al. [72] suggested, on the basis of molecular data, that common bean was domesticated independently both north and south of the Isthmus of Tehuantepec, which would fit with these early records. However Kwak et al. [73] argued, also from molecular data, that common bean was domesticated once only, near the northern frontier of Mesoamerica. Wild *P. vulgaris* occurs sporadically throughout Mesoamerica, so could have been domesticated more than once.

Many traditional Mexican landraces of common bean have retained the climbing habit characteristic of wild beans. Mixtures of four to six landraces are often sown in the same hill as maize, to climb up the maize stems. Components of these mixtures germinate at different rates, so the bean population is to some extent buffered against uncertainties in the spring rains and the harvest period is also extended [74]. Non-climbing bush beans, on the other hand, are today not co-cultivated with maize or other competing species and are not grown as mixtures of landraces. The plants germinate and grow at the same rate and all plants in the plot can be harvested simultaneously. Remains of some complete plants of common bean from the Ocampo caves in Tamaulipas were considered to show the bush habit [69]. They were directly dated to 1300–1250 BP, but the archaeological record provides no data on how these bush beans were grown or why the non-climbing habit was selected.

The Formative was also the period during which maize became prominent in the human diet. On the Pacific coast lowlands of southern Mexico and Guatemala, large settled villages developed by about 3600 BP, associated with the Mokaya, which means “maize people” in the Mixe-Zoquean language [75]. Charred remains of maize and beans showed that the Mokaya cultivated crops, but human bone composition suggested that maize was only a supplement in a diet that included fish and animals from the surrounding forests [76].

On the Gulf side of the Isthmus of Tehuantepec, the early Olmec were contemporaries of the Mokaya, developed in a similar ecological setting and, like the Mokaya, subsisted primarily on resources from the floodplain with some limited cultivation of maize [77, 78]. As the Olmec population increased, perhaps as a consequence of increased dependence on agriculture, their settlements shifted away from the seasonally flooded plains to uplands such as the Tuxtla Mountains [78], where, at the site of La Joya, ash from a volcanic eruption about 2150 years ago buried ridged fields assumed to have been used for cultivation of maize [79].

Other species grown or exploited by the inhabitants of La Joya included avocado, guava (*Psidium guajava*), coyol palm (*Acrocomia mexicana*) and mamey sapote (*Pouteria sapota)* [79]. Papaya (*Carica papaya*) and *Annona* sp. have been added on linguistic grounds to the list of fruits known to the Olmec [80]. Most, if not all, of these species appear native to the Mesoamerican lowlands, and wild populations are difficult to distinguish from relics of cultivation. Where human selection has resulted in morphological changes, these are usually in traits that are unlikely to be preserved archaeologically, such as fruit colour, quality or texture of the flesh. The status of these species among the Olmec (i.e. wild, cultivated or at least partially domesticated) cannot be determined from the archaeobotanical specimens available, but VanDerwarker [79] noted that the ratio of fragments of tree crops to fragments of maize and bean in flotation samples from La Joya increased through time. She therefore suggested that as the Olmec became more sedentary and more dependent on cultivated crops, they created more managed forests, managed fallows and gardens.

Between about 3550 and 3150 BP more sophisticated pottery appeared in the Pacific lowlands of southern Mexico and Guatemala and also further north in western Mexico. The antecedents of this pottery are unclear, but contacts with northwestern South America have been suggested [1, 81, 82]. These contacts could have provided a route for introduction of South American domesticates to Mesoamerica and vice versa [83].

Probably the most significant of these South American domesticates was manioc (*Manihot esculenta*), shown by molecular data to have been domesticated in southwest Amazonia [84, 85]. Brown et al. [86] were able to reconstruct terms for manioc in all the proto-languages of Mesoamerica, including Proto-Otomanguean, a highland language dated to 6591 BP. They therefore argued that domestication and dispersal of manioc occurred before the general development of villages based on farming. Single pollen grains of *Manihot* have been reported from Archaic levels in cores from San Andrés in Tabasco [52], and Cob Swamp [57] and Cobweb Swamp [87] in Belize. However, several wild species of *Manihot*, not implicated in the origin of domesticated manioc, occur in Mesoamerica and *M. esculenta* cannot be distinguished from these by pollen alone [52]. Furthermore, single pollen grains are not convincing evidence of early cultivation of manioc, since they may be modern contaminants or may have filtered down from higher levels of the core. Arnold [78] cited an unpublished report of manioc phytoliths from the Olmec site of San Lorenzo, but nevertheless concluded that there was very little evidence that manioc was grown by the Olmec. Some samples of charred roots, one directly dated to

2450 ± 70 BP, from the Early Maya site of Cuello in northern Belize were identified as manioc from their morphological and anatomical characters [88]. Manioc was certainly a staple among the Classic Maya, but further work is needed to reconcile the limited archaeological record of manioc with the conclusion from palaeobiolinguistics that it became widespread in Mesoamerica in the Archaic.

Another species that originated in South America is cacao (*Theobroma cacao*). It is still unclear whether this species spread to Mesoamerica by natural means or by dispersal by humans. Linguists have argued that cacao was part of the cultural inventory of the Olmecs [80] and have tentatively suggested that it was important to highland people by 3200 BP [19]. Traces of theobromine (one of the alkaloids present in cacao seeds and responsible for the stimulant effects of cocoa and chocolate) have been found in potsherds from the Olmec site of San Lorenzo on the Gulf Coast and also from a Formative site on the Pacific coast [89, 90], in the region known as the Soconusco, noted for cacao production both pre- and post-Conquest. However, traces of theobromine in potsherds are not unequivocal evidence for the presence of *T. cacao*. A chocolate drink can also be made from seeds of *T. bicolor*, a species known as pataxte, indigenous to Mesoamerica, and still cultivated in Veracruz, Tabasco and Chiapas although its seeds seldom enter world trade because they produce an inferior chocolate [91]. However, pataxte may have been more highly valued in the past. According to the creation myth in the Popol Vuh, the sacred book of the Quiche Maya, the foods that were to form the bodies of humans were found in the Mountain of Sustenance "and so they were happy over the provisions of the good mountain filled with sweet things, … thick with pataxte and cacao, countless zapotes, anonas, jocotes, nances …" [92]. On the evidence of the potsherds, the technique of making a drink from *Theobroma* seeds was known to the earliest civilisations of Mesoamerica but it remains to be demonstrated conclusively that this drink was made from *T. cacao* in Olmec times.

Classic Period, About 1750–1000 BP

After the decline of the Olmec, several nation states arose in different parts of Mesoamerica, notably the Zapotec in the Valley of Oaxaca, the inhabitants of Teotihuacán in the Basin of Mexico and the Maya in the Yucatán peninsula, Guatemala and adjacent areas. All were characterised by large settlements that qualify as cities. Their urban populations were sustained by agriculture, trade and tribute derived from conquest of neighbouring tribes. Maize, beans and squash were all well-established crops, but other species that were almost certainly domesticated earlier have also been recovered. For example, part of the residential area at Teotihuacán yielded storage vessels dominated, predictably, by carbonised maize, but also by carbonised *Chenopodium* [93]. This is the earliest record of harvest and storage of *Chenopodium* on a sizeable scale.

The best picture of crops and agriculture in the Classic Period comes from ongoing excavations at the Maya village of Cerén in El Salvador. This village was abandoned after eruption of a nearby volcano some time between AD 585 and AD 600. So many details of everyday life have been preserved that Cerén is now a World Heritage Site. Consolidated ash covered fields outside the village and retained impressions of the plants growing in the fields at the time of the eruption [94]. Some contained maize, while manioc had recently been harvested from another, leaving some tubers that had been missed during harvesting. The field had then been replanted with segments of stem inserted horizontally, in the same way that manioc is propagated today. A kitchen garden contained rows of another root crop, malanga (also known as yautia or cocoyam; *Xanthosoma* sp.) [95]. A trunk of cacao with an attached inflorescence [96] demonstrated unequivocally that *Theobroma cacao* was used by the Maya. A garden of agave close to a house complex possibly represented a food crop, but agave fibre was also used as twine to tie a fence made from *Tithonia* stems and to make a cloth covering for a kitchen vessel [97]. Bottle gourds and chile peppers had apparently been hung from rafters in a kitchen area for drying or storage, while one pot contained maize kernels that were seemingly being soaked for grinding next day. Other pots contained beans, mostly domesticated but often including some wild *Phaseolus vulgaris* [97]. The latter may actually have been weedy hybrids between wild and domesticated beans. These are common in areas of traditional agriculture. Zizumbo-Villareal et al. [98] described how traditional farmers in west-central Mexico planted mixtures of landraces of common bean and harvested and stored these as mixtures that were separated into their components only as required for consumption or other purpose. The finds at Cerén may indicate that this practice of storing mixtures of beans for later sorting may extend back at least to the Classic Maya.

Seeds and rinds of squash were recovered from both kitchen and storeroom contexts and identified as the lowland-adapted *Cucurbita moschata* rather than the highland-adapted *C. pepo*. Some of the seeds were associated with a metate, suggesting to Lentz et al. [97] that the oil-rich seeds were ground, either for consumption or to extract the oil. Cotton seeds were also found on a metate, as well as in other contexts, so Lentz et al. [97] suggested that these too were used as a source of oil. Coe [99] considered that edible oils were not used in Mesoamerican cooking before European contact, but plant oils have cosmetic and medicinal as well as culinary uses.

Cotton fibre, cloth and spindle whorls of a size appropriate for spinning cotton were found in various contexts [97]. Stark et al. [100] considered that evidence for cotton spinning, in the form of specially manufactured spindle whorls, appeared first in the Gulf Coast lowlands of Veracruz. Formative Period figurines from this region were nearly nude, whereas Classic Period figurines were frequently shown clad in textile-like garments, suggesting to Stark et al. [100] that selection of more productive cotton and its increased cultivation may have been a response to demand from a cultural elite. They also pointed out that cotton, like cacao seeds, was one of the few widely accepted media of exchange or proto-money and the durability of cotton fibre and textiles, and their favourable weight-to-value ratio, made them feasible trade items with remote highland areas.

Post-Classic Period, 1000 BP to the Spanish Conquest

By the time of the Spanish Conquest, all the principal crops of Mesoamerica had been domesticated and attention had apparently switched to diversification. Diversification generates variation within crop species and often results from deliberate human selection, usually after domestication, whereas domestication involves differences between crop and wild populations and frequently results from unconscious selection exerted by the new environment produced by cultivation [101, 102]. Early historical accounts, such as those of Fray Bernardino de Sahagun for the Aztecs, or Bishop Diego de Landa for the Maya, described considerable diversity, especially among annual seed-propagated crops. Sahagun described eight sorts of maize, 12 different kinds of beans, and five kinds of cotton. Even among vegetatively propagated crops such as sweet potato, several distinct types existed.

A few domesticated species do seem to have appeared in Mesoamerica only in Post-Classic times. Papaya has been included, on linguistic grounds, among the fruits known to the Olmec [80], but has no archaeological record in Mesoamerica, though its numerous hard seeds should preserve well. It was among the fruits presented to early European explorers sailing along the coast of Yucatán [99]. Wild papaya occurs from Costa Rica north to Guatemala and Mexico [103] and may have been domesticated south of the major regions of plant domestication in Mesoamerica.

Pineapples (*Ananas comosus*) were also among the fruits offered to Europeans exploring the coast of Mexico and were recorded in Guatemala and southern Mexico early in the seventeenth century [104]. Pineapple undoubtedly originated in South America. The only archaeobotanical record in Mesoamerica is an extremely questionable one from human coprolites from Coxcatlán cave in the Tehuacán valley, some time after 2200 BP ([24], but see also [25]). Whether pineapple reached Mesoamerica through the early contacts with South America that introduced manioc, or whether it spread later, possibly via the West Indies, remains an open question.

Peanut (*Arachis hypogaea*), like pineapple, originated in South America and, again like pineapple, has been reported archaeobotanically only from Coxcatlán cave in the Tehuacán valley (five specimens, all later than 200 BP) [20]. None of the specimens has been directly dated so, given the amount of disturbance documented for this site, their age needs to be confirmed. The Nahuatl name for peanut, cacahuatl, translates as "cacao that grows underground". Because peanut has only a compound name, involving comparison to another crop, Coe [99] considered that it was probably a recent arrival in Post-Classic Mesoamerica.

Discussion

Plant domestication in the highlands of Mesoamerica seems to have begun in two somewhat different contexts: among nomadic hunter-gatherers in semi-arid valleys, and among sedentary groups around the shores of lakes.

In the semi-arid highland valleys, cultivation provided a supplement to the diet and did not involve exclusively food plants. The earliest domesticated plants so far recovered are bottle gourd and *Cucurbita pepo*, both dated to about 10,000 BP. Dried fruits of bottle gourd furnished valuable containers, but bottle gourd is unlikely to have been primarily a food plant although young shoots and young fruits of non-bitter forms can be cooked and eaten. Bottle gourd is unknown in the wild anywhere in the Americas, so must have been domesticated elsewhere, in a region and at a date still unknown. The antecedents of the Mexican lineage of domesticated *Cucurbita pepo* are also uncertain, although this species may have been domesticated in or near the Valley of Oaxaca [17, 18].

Agave and *Opuntia* were also present from the earliest levels of both Guilá Naquitz cave in the Valley of Oaxaca and the Tehuacán Valley caves but it is not clear whether they were cultivated or merely exploited. Despite millennia of use by humans, both have remained only incipiently domesticated. Nevertheless, Gentry [105] suggested that *Agave* had as much to do with the beginnings of agriculture in Mesoamerica as any other genus, while Parsons and Darling [106] considered that development of agriculture in the cold dry highlands, where agriculture based on annual species is limited to one crop per year, was dependent on cultivation of *Agave* as a complement to seed crops for both food and fibre.

It now seems that, despite early beginnings of cultivation in the semi-arid highland valleys, these were unimportant in the domestication of the major Mesoamerican crops. Except possibly for *Cucurbita pepo,* grain amaranth and avocado, most crop species that became significant in the archaeobotanical record of the Tehuacán Valley had already been domesticated elsewhere [27].

In a different ecological setting, on a lake shore in the Basin of Mexico with plant and animal resources available year-round, Niederberger [46] found that a sedentary lifestyle developed about three millennia earlier than in the Tehuacán Valley. Plant remains recovered from the earliest phase of her excavations (about 8000–6500 BP) included seeds of *Amaranthus* and *Physalis*, one seed of *Cucurbita* and some grains of teosinte, though Mangelsdorf [107] considered that these last were probably intrusive. Although it is not clear whether these species were domesticated, cultivated, or merely exploited, all are weedy annuals adapted to colonising the bare soil that results from a receding lake margin during the dry season or from activities associated with permanently occupied human settlement. Niederberger [46] suggested that at this site there was initially no clear distinction between food gathering and food production. This is similar to the beginnings of cultivation in the Valleys of Oaxaca and Tehuacán, and fits the category of low-level food production defined by Smith [108].

In a similar lake shore setting, the Balsas basin project [39, 41] in western Mexico aimed to gather evidence on the domestication of maize and thus settle controversy about whether maize and maize agriculture originated in highland or lowland Mesoamerica [30, 53]. At an altitude of about 700 m, the Balsas basin is perhaps best regarded as mid-altitude, rather than highland or lowland, and is home to the populations of teosinte suggested by molecular data as those closest to the wild progenitor of domesticated maize [45]. Exactly how or when conscious or unconscious human selection converted the female infructescence of teosinte, with its edible grains enclosed in a hard indigestible fruitcase, into the ear of maize, with its grain exposed on the surface of the cob, remains an enigma. Some important alleles of the genes controlling these differences exist as standing variation in wild populations of teosinte, for example, the maize allele of the gene *teosinte branched1* (*tb1*), which controls branching of the whole plant and also of the female inflorescence. Recent work on *tb1* suggested that these two phenotypic effects are influenced by different components of the control region of *tb1* [109]. Individuals of teosinte may carry change in one or the other component but not both. Both changes are present, but uncommon, in Balsas teosinte and also in teosinte from higher altitudes. Zhou et al. [109] suggested that the two changes predated domestication and were brought together by hybridisation, after which the maize phenotype was fixed by selection under domestication. A second gene important in the evolution of the ear of maize is *teosinte glume architecture1* (*tga1*), which controls hardness and curvature of the glumes enclosing the grain. The maize allele of *tga1* has not been found in teosinte, so may have arisen and been selected only after *Zea mays* was taken into cultivation [110].

Maize agriculture apparently spread relatively rapidly through lowland Mesoamerica between 4700 and 4200 years ago [47] but maize was at that time only a minor component of the diet. The anomaly of why a minor food crop should spread so rapidly remains unexplained, though it has been suggested that its principal attraction was the sweet juice in the stems [42, 43]. This juice could be fermented to produce an alcoholic drink, or evaporated to produce sugar. As a grain crop, maize did not become a staple until the Formative Period. Various reasons have been suggested to explain this delay. The complexities involved in the evolution of the maize ear, requiring hybridisation between different accessions of teosinte and also occurrence and selection of appropriate mutations, may have been one reason. Another may have been the low grain yield of the earliest maize. Bray [111] cited information from Kirkby that the Zapotec did not consider it worth growing maize if the expected yield was less than 200 kg of shelled kernels per hectare. Below this level, maize cultivation was considered less productive than gathering wild resources, such as pods of mesquite (*Prosopis juliflora*); above this level, clearing mesquite scrub to plant maize becomes worthwhile. Bray [111] considered that this critical threshold of maize productivity was crossed only about 4000–3500 BP.

The Formative Period was marked also by the first occurrence of pottery in Mesoamerica and the appearance in the archaeological record of domesticated beans, at about the same time in the highlands and lowlands. As noted by Smith [112] and others, although maize, beans and squash are now regarded as the characteristic triad of New World agriculture, and are often cultivated together, each species was actually domesticated in a different part of Mesoamerica, separated by several millennia in time.

The Formative is also a period in which some archaeologists have claimed significant contact between Mesoamerica and South America. Domesticated plants moved in both directions. The most significant introduction into Mesoamerica was manioc, which became a staple among the Maya [94]. Cacao may have spread by natural dispersal, but the chocolate drink made from it assumed considerable ritual and ceremonial importance among Mesoamerican civilisations from the Olmec onwards [90]. Tomato (*Solanum lycopersicum*) is another South American species that may have spread naturally or with the aid of humans to Mesoamerica, where much of the diversity in the crop originated [113]. There is no archaeological record of tomato, though tomato seeds survive passage through the human digestive system so should be recoverable in coprolites and among macroscopic remains. This may suggest that tomato reached Mesoamerica relatively late in prehistory, as did two other South American domesticates, pineapple and peanut.

Carl Sauer [9] argued that agriculture originated among sedentary groups, subsisting primarily by fishing, in the lowlands of the humid tropics, and that the first crops cultivated were vegetatively propagated species grown for their starch-rich underground storage organs, not annual seed-propagated crops. His influential views cannot yet be fully tested for Mesoamerica. There is no evidence that cultivation of root crops preceded cultivation of seed-propagated maize, beans and squash, or that agriculture in the lowlands preceded agriculture in the highlands. However, it has proved very difficult to locate Archaic period sites in the lowlands, because they may be buried under sediment deposited by rivers or inundated by post-glacial rises in sea level [55, 114]. Furthermore, it is only under exceptional circumstances, such as those at Cerén, that the importance of root crops to a particular culture can be assessed. Underground storage organs do not preserve well, so macroscopic remains are seldom recovered by archaeologists. Storage organs are often consumed after boiling or roasting, so may not leave traces of their preparation in the form of starch grains on grinding stones. Examination of the teeth of human skeletons for phytoliths or starch grains, which has yielded evidence of diet in the Andean region, has not yet been carried out in Mesoamerica. It is notoriously difficult to prove a negative, and the difficulty of proving that lowland root-crop agriculture did not precede highland seed-crop agriculture is compounded by the notoriously incomplete archaeological record.

The emerging picture of plant domestication in Mesoamerica is currently of a slow beginning, as a supplement to other forms of subsistence: an evolution in lifestyle rather than a revolution. More species were added to the roster of crop plants in different places and at different times. Although Mesoamerica as a whole is considered a centre of origin of agriculture [115], domestication seems to have taken place virtually all over this region, not in a single locality. Some species, such as maize and beans, appear in the archaeological record as fully domesticated, without any apparent intermediates to show how human selection transformed a wild species into a domesticate. Other species, such as maguey, the giant cacti and many of the tree fruits, have been little changed by human selection and have remained at the stage of incipient domestication.

Domestication was followed, in many crops, by impressive amounts of diversification. Some of this was recorded by early observers such as Friar Bernardino de Sahagun, but how and why the pre-Columbian farmers of Mesoamerica developed and preserved so much diversity in their crops, and thereby provided their conquerors with genetic resources that are still valued today, remains a matter for speculation only.

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Chapter 10
Cultural Motives of Plant Management and Domestication

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Abstract We analysed the diversity of forms in which human communities of the Tehuacan Valley manage their plant resource, as well as the motivations and factors influencing how such management forms are and how intensely held. We explored and identified ecological, sociocultural, economic and technological factors that influence how the management forms and their intensity are, as well as the causal relationships between these factors and management decisions. Particularly, the factors mentioned were analysed in the context of scarcity and uncertainty in the availability of edible plant resources, as well as individual and collective responses that implement human beings to ensure their use. It was analysed with particular depth how people perceive uncertainty in availability of edible resources and the various ways in which they face it, how they build their decisions and develop techniques to mitigate the effects of such uncertainty. Most management forms involve artificial selection at different intensity levels.

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We characterized the type and intensity of management based on the following indicators: (1) complexity of the practices involved, (2) occurrence of artificial selection, (3) strategies, techniques and collective social regulations implemented in management, (4) energy invested in terms of labor, fossil energy and (5) amount of resources obtained per area unit. We found that the lowest values of management intensity corresponded to species under simple gathering or tolerance, mostly annual abundant plants occasionally consumed by few people. In contrast, the highest levels of management intensity were recorded in species with economic importance, mostly perennial with recognized variants whose management requires using tools, and which are protected by collective regulations. Nearly 67.6 % of variation of the management intensity was explained by risk variables, such as length-span of life cycle, reproductive system type, distribution, number of plant parts used, number of management forms and using regulations. Thus, people make decisions at individual or community levels involving strategies for controlling ecological and/or cultural factors in order to decrease uncertainty. Understanding current management processes seeks a better understanding of the history that led to the management and domestication of nature. It aims at providing more arguments for interpretations of archaeological data about the origin of management, domestication and agriculture. But also, it aims at contributing to the design and construction of future sustainable management strategies.

Keywords Plant management • Domestication • Uncertainty • Food resources • Tehuacan valley

Introduction

Until 12,000 to 10,000 years ago, the humanity lived mainly based on hunting, fishing and gathering of plants, mushrooms and other forest products [1–3]. But by the end of the Pleistocene, the average temperatures of the planetary surface started to rise, and with that fact the new period known as Holocene involved significant ecological changes, among them the colonization of new areas by a number of plant species as well as migration and extinction of a numerous animal species that supported the hunting activities of humans [4]. Human beings progressively adapted their lives establishing new forms of natural resource using; particularly in the cases of biotic resources, numerous species decreased their known availability and some others were unknown at the new environments; it is possible to assume that the Holocene transition was a period of relatively rapid environmental changes and uncertainty in availability of resources for human subsistence. Such changes influenced in turn the transition towards other forms of interactions between societies and nature and were particularly responsible of processes that led to the origins and development of agriculture [1, 5–9]. Agriculture was a new strategy in human history combining old systems of modifying the environments according to human needs, together with a process of modelling organisms according to human desires: domestication [10].

Until recently, the relation between humans and plants was conceived as a great dichotomy between gathering and agriculture [11, 12]. However, archaeological and ethnobotanical researches during the twentieth century provided progressively numerous examples of the occurrence of a broad spectrum of interactions that cannot be catalogued *sensu stricto* neither as gathering nor agriculture [10, 13–15]. This information determines that at present researchers have to consider the perspective of other types of management practices, including different forms of carrying out domestication of plants. The evidence about such a broad spectrum of types of plant management leads to the thinking that probably were not only responses to climate changes or to increasing density of human populations the main factors conducting to agriculture, but also technological innovations as consequence of creativity and decisions made by human persons in their daily life [16].

It is necessary to consider that plant management and domestication are processes that not only occurred in the past, but these are ongoing current processes occurring continually, even in plants with advanced levels of domestication. Also, it is necessary to consider that these processes may evolve gradually or suddenly, depending of the nature of the reproduction system of the plants people manage, and depending on the human cultural actions involved in management [10]. Changes associated to domestication constitute adaptive responses of both plants and humans managing those plants according to specific ecological and sociocultural conditions, which are greatly dynamic throughout time [17], actually much more dynamic than natural changes determining natural selection and adaptation. For this reason, domestication has been considered by several authors as rapid process of evolution [8].

The Diversity of Forms of Interactions Between Humans and Plants

Ethnobiological and archaeological researches have provided valuable information characterizing different forms of interactions with plants practiced by humans. These practices appear to represent a gradient of complexity of actions, from those occasional and simple to those systematic and specialized [7, 10, 13–15, 18–22]. Particularly, in México an increasing number of ethnobotanical studies have documented different forms of interaction between humans and plants at different levels or organization (individuals, populations, communities and ecosystems), as well as in different evolutionary contexts (wild, weedy, ruderal and domesticated) [10, 13, 15, 21, 23, 24].

Such interactions are not properly simple gathering (in the sense of harvesting plant products from nature) neither agriculture (management of domesticated plants in anthropogenic ecosystems); their intermediate characteristics have conducted to several authors to consider them as forms of "incipient management" and the domestication processes associated to these type of management as "incipient domestication". These types of management may be conducted in situ or ex situ [10]; in the first case, in situ management includes all practices carried out in the natural vegetation or forests where wild plants may be intervened by humans with different purposes; but also, this management type may occur on weedy or ruderal plants adapted to environments under recurrent human disturbance [25]. Ex situ management is conducted out of the areas of natural plant populations and communities, these are carried out in environments under human control (agricultural plots, homegardens).

The techniques of in situ management more commonly recognized are:

1. Tolerance, which consists in leave standing wild plant species or special phenotypes of these species that are particularly valued by humans because of their characteristics that make them good resources. This practice is common in traditional rural communities when people clear the forest to establish new crop lands or as part of the daily life activities before the crop sowing or during the practices of weeding.
2. Promotion. This practice consists in conducting activities directed to increase the density and availability of useful wild plant species in natural habitats or weedy plants in agricultural areas. Examples of these practices are the sowing and vegetative propagation of useful plants within the areas occupied by their natural or weedy populations.
3. Protection, which consists in actions that favour the permanence of some particular plants; for instance, people use to remove competitors and herbivores of some plant species or particular phenotypes, also the use to protect them against pests and environmental factors such as excessive solar radiation, frosts, shade, or they may remove ground in order to favour aeration and other labours favouring their maintenance.

The techniques of ex situ management consist mainly of seed sowing and transplanting of entire plants or vegetative propagules from wild or weedy areas towards agricultural plots or homegardens. Examples of both in situ and ex situ forms of incipient management can be consulted in several ethnobotanical studies. Particularly, examples among the Rarámuri [26, 27], the Teenek [13]; several regions of México [24]; the Balsas River Basin and the Tehuacán Valley [10, 21, 22]; agaves from Colima and Jalisco [28] and the Tehuacán Valley [17, 25].

Both in situ and ex situ management forms may involve processes of artificial selection, some of which have determined morphological, physiological, reproductive and genetic divergences between wild or weedy and managed populations and, therefore incipient processes of domestication associated to silvicultural and agricultural forms of management [10].

Management Intensity

Management can be defined as those practices and decisions made consciously or deliberately by human beings in order to transform, recover or conserve elements, ecosystems or processes occurring in those systems in order to satisfy human needs, cultural purposes or general desires [17, 25]. Because many plant resources are managed according to their biological and ecological characteristics (life cycle, type of reproductive system, distribution, abundance, among others) and according to their importance for a human culture (for instance, resources may be preferred or not, desirable or not, demanded or not, substitutable or not), it is possible to expect that not all plants are equally managed neither in form nor in intensity. Management intensity can be defined as a relation of specialization and complexity of the practices carried out on plant or animal resources [29]. The management intensity involves combined actions generally investing higher effort and complexity of practices and social agreements in order to ensuring or increasing the availability (in terms of both quantity and/or quality) of plant resources [30].

Ethnobotanical studies in Mexico have analysed management intensity particularly with edible plant species [17, 25, 29–31]. The first studies involved indicators of intensity based on the type and number of practices carried out, as well as the number of persons carrying out those practices in a social context [29]. Later on, Casas et al. [30] and Blancas et al. [25] suggested a framework of management intensity based on indicators commonly used by agroecologists to analyse intensification of agricultural systems [32]. Blancas et al. [25], for instance, proposed as indicators of management intensity the estimation of the energy invested in the management system (amount of work, number of persons involved, time invested in labours, use of fuel and other inputs); the complexity of the strategies (from individual decisions to social agreements and regulations of actions at communitarian and or regional levels), types of tools and techniques (from sticks and stones to machines), as well as the productivity, estimated in terms of the amounts of products obtained per area unit [25, 30].

At the same time, we developed indicators of risk in the availability and permanence of the resources and systems they form part. We considered that such risk indicators should include ecological and sociocultural aspects. For instance a natural vulnerability associated to scarcity or local distribution of resources may be increased by a high demand in markets or a high value promoting their high harvesting. These indicators allow detailed typologies of risk, similarly as the detailed typologies of management intensity through indicators such as energy invested, complexity of tools and management strategies and productivity as referred to above [17, 25]. With both typologies it would be possible to explore the relation between amount of risk and management intensity as cause-effect processes in current real cases of resources and ecosystem management.

Uncertainty in the Availability of Plant Resources as Motive of Management

Several archaeologists have proposed that the intensification of management of plant and animal resources was a response to conditions of uncertainty in their availability, which was associated to changes in climate, extinctions of mega-fauna and/or increasing of human populations [1–3, 33]. This is for instance one of the most popular theories about causes to explain the origins of agriculture in several areas of the world at relatively similar times. However, it is not only the implicit recognition of the scarcity of a resource what is important. In fact the scarcity of a resource is an ecological issue involving for instance distribution, abundance, rapidness of reproduction and growth. But it is also a sociocultural issue since their cultural and economic value, their role in household subsistence, among other aspects influence the meaning of what is scarce or how much affects the scarcity of a plant resource. Scarcity, from a social perspective is therefore relative to the meaning of a resource to people. Independently of ecological parameters, a resource is scarce when it is insufficient to satisfy a need; it is also scarce when no other resource can substitute its benefits. Inter-annual or long term changes in temperature, pluvial precipitations, incidence of pests, populations of pollinators and dispersers, among other factors, may be indicators of the possible changes in the availability of a meaningful important resource. These changes, according to oral traditions and direct experiences modulate a perception about uncertainty of the resources availability. Uncertainty may be therefore related to sudden scarcity associated to human disturbance, unpredictability in the availability of resources associated to changes in biophysical factors.

Uncertainty constitutes a conceptual framework necessary to understand the causes of intensification of plant management. The diversity of management forms and their intensity suggest that management has not been an episodic event but a continual adjusting of ways for accessing to plant resources [25]; also, that management and domestication are not themes of the past times but ongoing processes which can be starting even at present, continuing those started in the past or even losing some of them already established in rural communities of Mesoamerica but that have decreased their importance or value for current societies.

The Tehuacán Valley as Setting for Studying Management in Relation to Uncertainty

The Tehuacán Valley is recognized as one of the arid zones of North America with the highest biological diversity. Valiente-Banuet et al. [34] and Dávila et al. [35] have recorded 2703 vascular plant species, but the current inventory surpasses 3000 species of plants distributed in 36 types of plant association within an area of 10,000 km^2. The region is also characterized by high cultural diversity with the presence of eight indigenous ethnic groups (Nahuas, Popolocas, Mixtec, Mazatec, Ixcatec, Cuicatec, Chocho and Chinantec), which constitute more than 30 % of the regional human population [36]. The cultural history of the region is more than 10,000 years old, and there is archaeological evidence of early human use of numerous species of plants and animals that presently occur in the area [2, 3]. The Tehuacán Valley is one of the areas of Mesoamerica more studied in relation to the prehistoric use and management of plants [1], as well as one of the regions of Mexico with more ethnobotanical information available [25, 36, 37]. In that region, archaeologists found a total of 83 plant species associated with human remains in caves of the area [5], as well as the earliest signs of domestication in some plant species [1]. Such a long history of interactions between humans and plants made possible that the Tehuacán Valley is now considered one of the vastest region of ethnobotanical knowledge, with more than 1600 plants used by the local cultures [37]. The history of interactions and the living culture of using and domesticating plants make the region an ideal setting for analysing the relations between risk and management intensity and support the interpretations of archaeologists with information based on current processes.

Plant Resources Management in the Tehuacán Valley

According with Casas et al. [36]; Lira et al. [37]; and Blancas et al. [25], in the Tehuacán Valley most of the plant resources identified are obtained from local forests through simple gathering; that is, occasionally harvesting plants or plant parts directly from ecosystems. However, a total of 610 plant species receive some type of management that is not only simple gathering. This number of species represents nearly 38 % of all useful plant species recorded hitherto, and nearly 22 % of the total flora of the Tehuacán Valley. These ciphers reveal the local knowledge of the flora, their inclusion as useful resources for satisfying human needs and an even deeper knowledge of the particular species that are managed, about which mechanisms of propagation, interactions, adaptability, are generally required. Local management involves a rich reservoir of techniques tested throughout long time but continually innovated. These local techniques are the basis for constructing effective strategies for using and conserving the local resources and ecosystems, and for attending the regional risk identified in particularly vulnerable plant species. A number of plant species have a restricted distribution, are rare, or simply have very slow growth rates. These and other features may be incentives for intensifying their management with the intention of making the resource available.

Table 10.1 shows that not necessarily those plant groups with higher number of plant species are necessarily those providing useful and managed plant resources.

Table 10.1 Families with the highest number species managed in proportion to the total flora and useful plants in the Tehuacan Valley

Family	Total of species (Dávila et al. [35])	Useful species (Lira et al. [37])	Species with management (Blancas et al. [25])
Poaceae	220	220 (100 %)	20 (9 %)
Asteraceae	345	195 (57 %)	52 (15 %)
Fabaceae	297	163 (55 %)	42 (14 %)
Cactaceae	74	67 (91 %)	62 (84 %)
Euphorbiaceae	106	38 (36 %)	16 (15 %)
Solanaceae	76	52 (65 %)	26 (34 %)
Malvaceae	56	25 (45 %)	12 (48 %)
Cucurbitaceae	21	20 (95 %)	14 (67 %)
Lamiaceae	95	31 (33 %)	10 (32 %)
Crassulaceae	49	30 (61 %)	36 (120 %)
Burseraceae	19	20 (105 %)	14 (70 %)
Agavaceae	25	23 (92 %)	23 (100 %)

These are the cases of the families Agavaceae, Burseraceae, Cactaceae, Crassulaceae, Cucurbitaceae and Malvaceae which include a high number of plant species used and managed, markedly higher than the natural proportion in which they are found in the context of the total flora of the region. For the contrary, the families Poaceae, Asteraceae and Fabaceae, which are highly rich and abundant groups in the region have less representatives in the useful and managed flora than expected if useful and managed plants were proportional to their abundance or appearance in nature. This information reveals that conspicuousness of the resources is not necessarily the cause of their use and management as resources. People recognize properties and value resources according to those properties and other attributes recognized by traditional botanical and ecological knowledge and made their decisions on what to use and what to manage in relation to a complex of socioecological factors.

Plant Management Types Documented in the Tehuacán Valley

The managed flora of the Tehuacán Valley includes 58 % of native species and 41 % of species introduced from other parts of Mesoamerica and other parts of the world. The different forms of ex situ management are practiced on nearly 65 % of the managed plant species, particularly through seed sowing, planting of vegetative propagules and transplanting of complete individual plants, generally young plants. Nearly 61 % of the managed species are in situ managed (note that the sum of percentages is higher than 100 % since several species are both in situ and ex situ managed). We have mostly documented practices of tolerance, promotion and protection (Fig. 10.1).

General Bases for a Typology of Plant Management

According to the theoretical elements discussed above, plant management may be carried out with a broad spectrum of levels of intensity and, also in theory, such spectrum should be in correspondence with the also broad spectrum of conditions of risk and uncertainty of those resources particularly meaningful to human communities. Figure 10.2 summarizes indicators for constructing typologies of risk and management intensity. Both general systems of criteria require to consider ecological aspects, as well as social, cultural, economic and technological factors influencing both the vulnerability of the resources and the nature of the management implemented.

We consider that recognition of intra-specific variants and practice of differential use and artificial selection on these variants are key criteria for classifying both in situ and ex situ management types. Consequently, the classification should include the following categories:

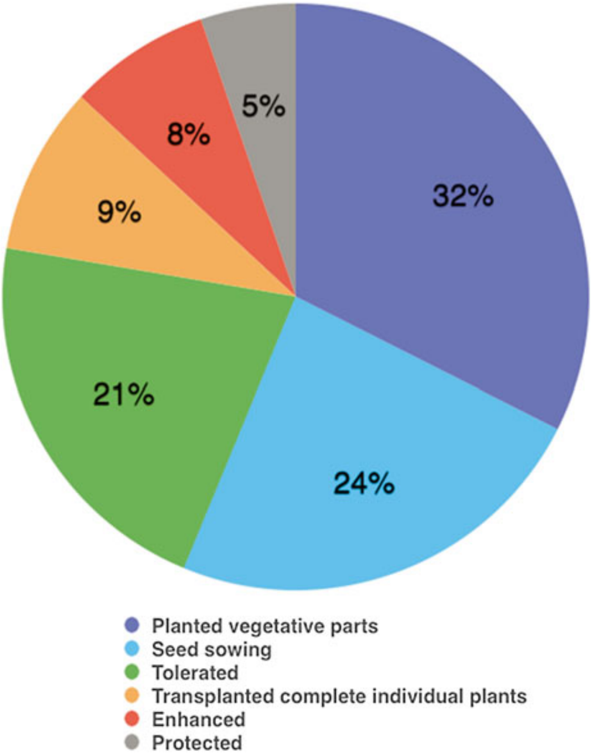

Fig. 10.1 Management forms documented in plants of the Tehuacan Valley

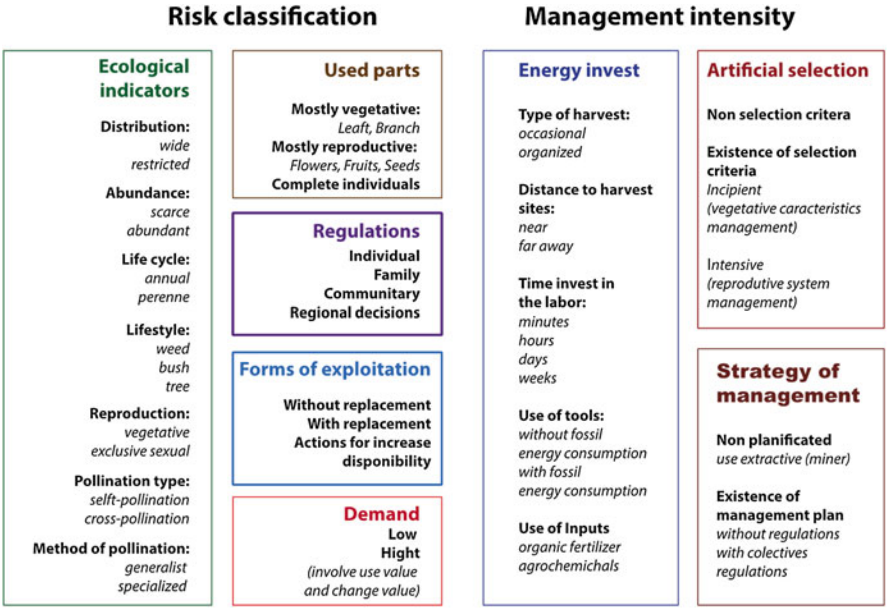

Fig. 10.2 General scheme representing general criteria to construct typologies of vulnerability of plants associated to use, and management forms of plants

Fig. 10.3 Gathering without recognition of variants. *Sambucus mexicana* (**a**), *Tigridia pavonia* (**b**), *and Vaccinium leucanthum* (**c**) are some examples of this condition

1. In situ *interactions*
    (a) Gathering without recognition of variants. Most wild species are gathered from natural vegetation without particular distinction of varieties or variations particularly preferred. Some are annual, others are perennial (Fig. 10.3).
    (b) Specialized gathering with appreciation of variants. The gathering is differential, since some individuals are preferred by collectors due to specific features (flavor, color, texture, size, presence or absence of toxic substances, etc.) (Fig. 10.4).
    (c) Tolerance without recognition of variants. These are species tolerated in maize fields, which are tolerated considering only their availability but not variant types. People practice weeding twice per agricultural cycle and decide to maintain these plant species because they are edible (Fig. 10.5).
    (d) Tolerance of recognized variants. Some variants are preferred and deliberately tolerated when peasants open crop fields to sow maize seeds; or when these are cleaned of weeds. This is the case of annual species of “quilite”. Many of these species are weeds and invade the crop fields. However, people distinguished variations in individuals, and these differences allow a differential removal of phenotypes that are undesirable (Fig. 10.6).

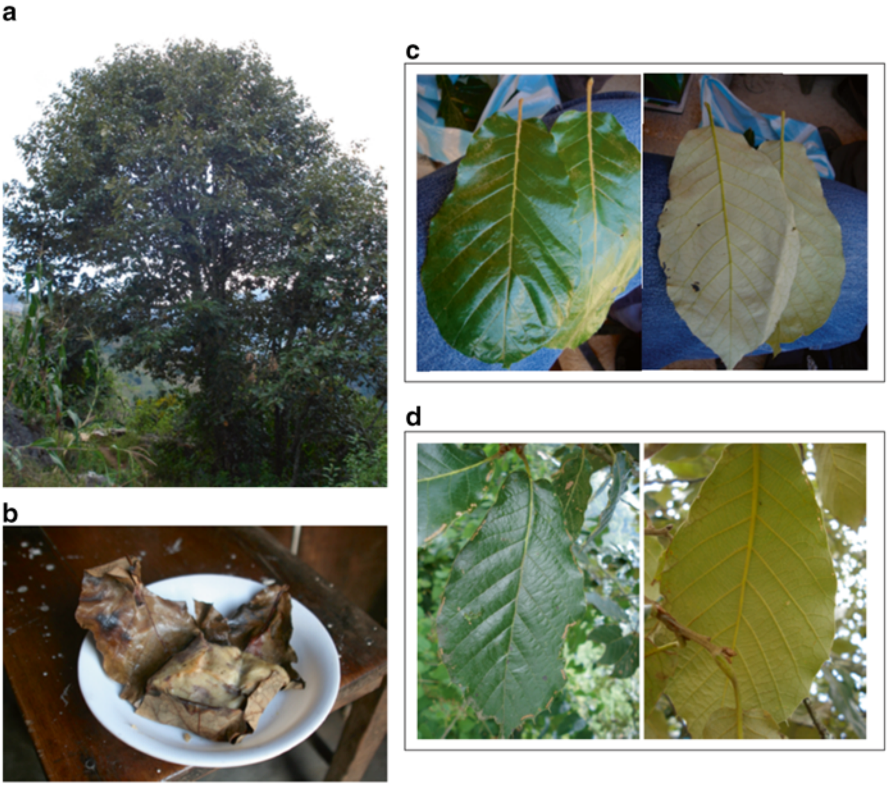

Fig. 10.4 Specialized gathering with appreciation of variants. *Quercus candicans* is a oak tree (**a**) whose leaves are used to cook "tamales" on celebrations days (**b**). Collectors recognized two variants: "lisa". Leaves large, thin, smooth. Leaf underside glabrous and bright. The surface of the leaf is light green (**c**); and "cucharuda". Leaves thick, leathery, spoon-shaped. Undersides densely tomentose, beam darker color (**d**). The "lisa" variant is preferred to wrap tamales, since it can be handled better and confers a nicer flavor. According to interviewees, the variety "cucharuda" is difficult to bend and confers bitter taste to "tamales"

(e) Enhancement without recognition of variants. This management type includes practices directed to deliberately increase abundance of a plant species but not specific variants (Fig. 10.7).

(f) Enhancement with recognition of variants. In this management type different strategies are undertaken to increase the population density of useful plants. This includes the sowing of seeds or the intentional propagation of vegetative structures in the same places occupied by populations of wild or weedy plants (Fig. 10.8).

(g) Protection without recognition of variants. This management practice includes actions directed to preserve wild plant resources that are not cultivated nor transplanted. In this type of action we include those practiced without distinction of variants (Fig. 10.9).

(h) Protection with recognition of variants. It consists of actions that seek to preserve wild resources without being cultivated or transplanted (Fig. 10.10).

Fig. 10.5 Tolerance without recognition of variants. An example of these plants is *Cleoserrata speciosa* (**a**). Its leaves consumed as greens (***quilite***) (**b**). Pods are collected, dried to the sun, and storaged in plastic bags; some plants are deliberately tolerated for ensuring seeds for the following agricultural cycle (**c**). Locally it is known as "Mabilquilitl" and it tastes delicious (**d**)

Fig. 10.6 Tolerance of recognized variants. For instance, *Raphanus raphanistrum* is a weedy species of which two varieties are recognized: "pubescent leaf" (**a**), purple flower, intense flavor and hard to digest; and "smooth leaf", white flower and sweeter taste. This latter variety is occasionally used as food. The pubescent variety is eliminated, since its consumption can cause stomach ache, or alternatively is used as fodder for turkeys, chickens, sheep, goats and pigs (**b**). Another example, but for a perennial species, is *Dasylirion serratifolium* (**c**), for which two varieties are recognized: individuals with purple inflorescence and larger flower buds; and individuals with white inflorescence and smaller flower buds. Both varieties are consumed (**d**) and traded (**e**), but if a person needs to make a choice she/he will selectively remove the variety with white inflorescences, since it produces a lower yield and has lower market prices

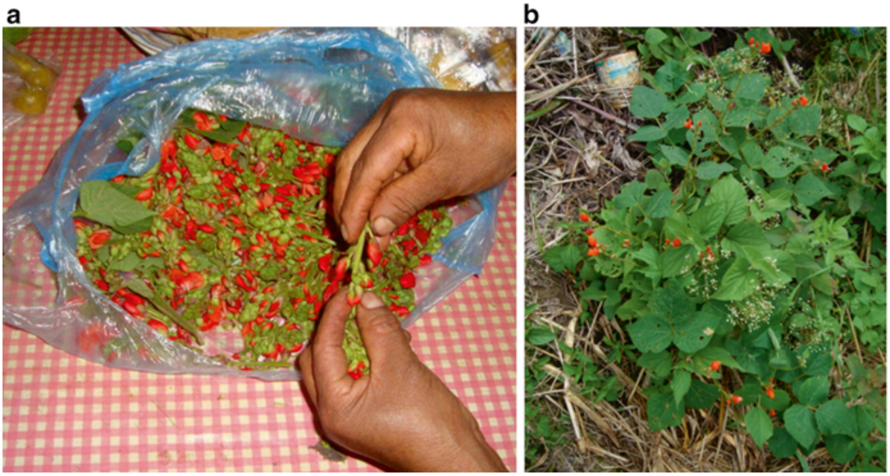

Fig. 10.7 Enhancement without recognition of variants. This is the case of *Phaseolus coccineus* whose leaves, flowers and immature pods are consumed as greens ("nezoquilitl") (**a**). Your management includes let standing plants in crop fields, particularly in areas surrounding the parcel (**b**). Also, people deliberately disperse its seeds in parcels where this plant species is absent

2. Ex situ *interactions*
   Some wild plants are cultivated in homegardens or in edges of crop fields. They are propagated by seeds, vegetative propagules, and in most cases by transplanting whole plants (Fig. 10.11).

Using the General Typologies of Management Intensity and Risk: A Case Study Among the Nahua of the Sierra Negra, Puebla

In the Tehuacán Valley there is a zone that for long time remained relatively isolated and has been scarcely explored by both floristic and ethnobotanical studies. This is the mountainous zone in the eastern area of the Valley locally known as Sierra Negra, which shelters a high floristic and environmental diversity in areas from elevations of 900 to 3600 m. Such a heterogeneous environments include vegetation types such as microphyllous shrub, tropical dry forest, pine and oak forests, cloud forest, and tropical rain forest, which are all used and managed by Nahua and Mazatec people. The history of interactions between local cultures and environments has been long and the local traditional botanical an ecological knowledge is particularly rich and deep. In the following sections we will summarize our studies documenting how local knowledge and techniques are used by people to face the hard conditions of uncertainty in the availability of crucial resources to satisfy needs of food.

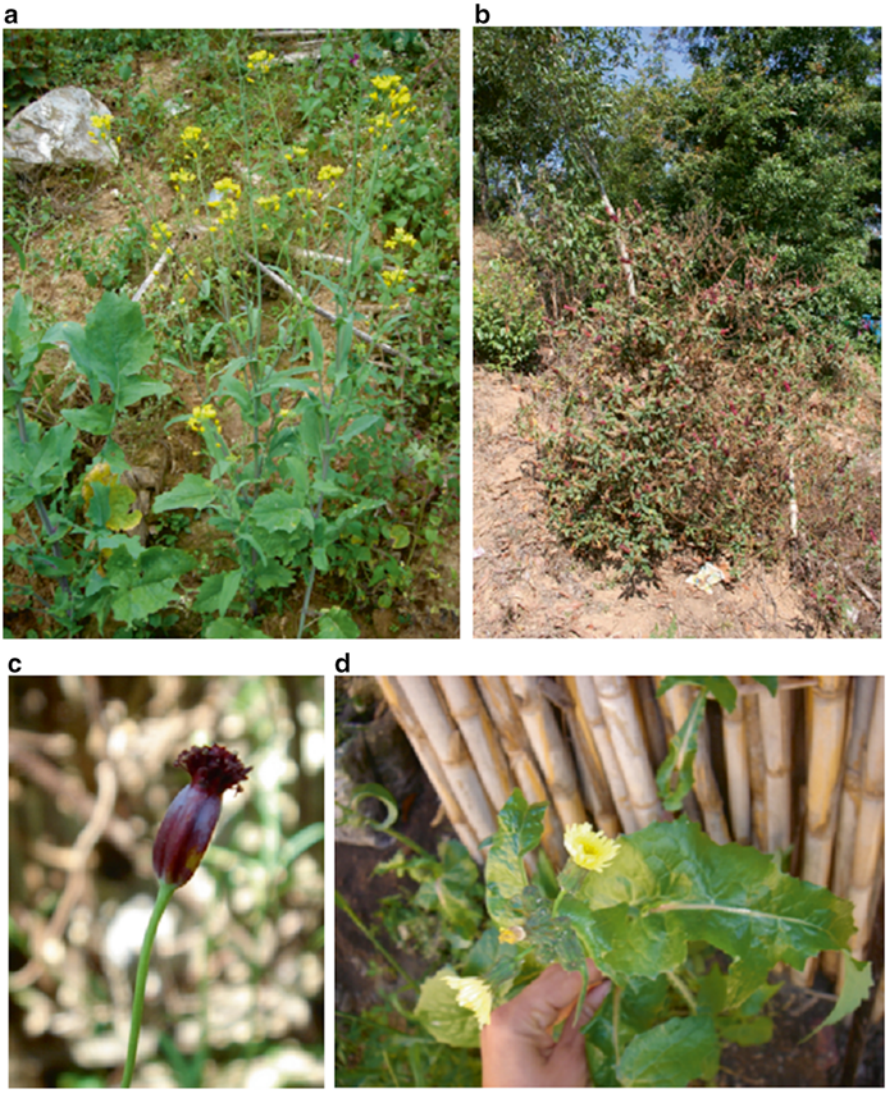

Fig. 10.8 Enhancement with recognition of variants. For instance, *Brassica rapa* (**a**) are enhanced in the crop fields. In addition, the seeds of *Phytolacca icosandra* (**b**), *Porophyllum linaria* (**c**), and *Sonchus oleraceus* (**d**) are scattered on roads and crop fields in fallow

Economic, Sociocultural and Ecological Factors Enhancing Plant Management

A plant species may be managed in different forms, with different intensities and levels of complexity of practices, depending on the ecological and cultural contexts [10, 15, 21, 36]. Therefore, analysing the economic and cultural values, as well as

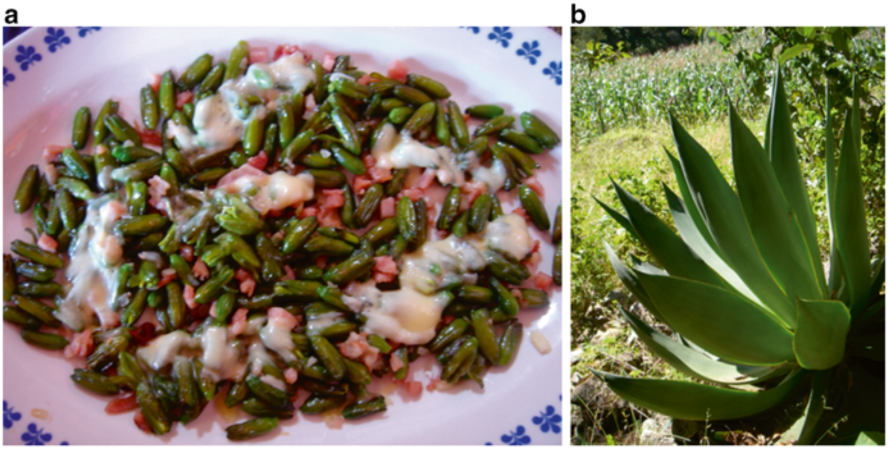

Fig. 10.9 Protection without recognition of variants. This is the case of *Agave obscura* whose flower buds are consumed as greens (**a**). Management is conducted by tolerating plants in areas cleared for agriculture (**b**). Their vegetative propagules are also separated from the mother plant and established and cared in areas convenient for people. Particular care such as weeding, clearing of competing plants, and removal of dry leaves in order to increase production of flower buds are occasionally carried out

the ecological role of particular resources in relation to management processes may be helpful for understanding motives of domestication; but also, for understanding the context and process of technological innovation. This latter aspect is particularly important in a time that requires higher efforts for constructing sustainable forms of using resources and ecosystems. In other words, understanding the motives and processes of construction of techniques not only provides an inventory of management techniques but also the possibility to understand the context in which they have developed, information that is particularly important for the purposes of developing appropriate technology for sustainability.

The cultural value of plant resources has been widely studied by a number of authors in a broad spectrum of cultural contexts and research methods have become a refined status with algorithms and relations taking into account use frequency, use preference, amounts of products consumed, use numbers, among other indicators [26, 38, 39]. The economic value has been evaluated directly in the markets through indicators such as prices, demand and supply balances, and their equivalence of exchange for other products in the interchange systems, among other indicators [40, 41]. Availability of resources has been evaluated through different indicators, including spatial aspects such as distribution and abundance, as well as temporal parameters such as life cycle, reproductive season, phenology, recovering capacity or resilience of affected populations and communities (in terms of population growth and recovering of diversity and ecosystem functions, among others), reproduction type, growth rapidness, among others [21, 25]. On the other hand, the management intensity may be estimated through indicators such as number and type of

Fig. 10.10 Protection with recognition of variants. For instance *Litsea glauscesens* is a wild species. Their leaves used as spice (**a**). In situ management is carried out by let standing trees when land is cleared for agriculture; also, young trees are transplanted to the surrounding areas of the parcels. Ex situ management is conducted y transplanting young plants from forests to homegardens. People recognize two varieties: the "smelly laurel" (**b**) which produces thin, small leaves with greyish back, aromatic and small flowers. The "cimarrón laurel" (**c**) variety produces wider and longer leaves with light colour back, less aromatic and with larger flowers than the other variety. The smelly variety grows in pine-oak and cloud forests, whereas the "cimarrón" variety grows in humid-warm areas with tropical forest. Management is different for each variety, people preferring let standing and transplanting the "smelly" variety. The people have increased leave collection, given their high demand in markets (**d**)

Fig. 10.11 Seeds sowing as in the case of *Chamaedorea tepejilote*, whose fruits are edible and the seeds are spread in homegardens, coffee plantations, and occasionally in cornfields (**a**). *Yucca elephantipes* is an example of propagation of vegetative parts to homegardens and surrounding areas of parcels. Branches for propagation are left drying for 2 weeks and then planted almost always as living fences (**b**); and transplantation of whole individuals is illustrated by *Crataegus mexicana* species is transplanted to crop fields (**c**). Besides eating the fruit, the whole plant is used to graft of fruit trees like apple and quince

practices (an approach to the complexity of practices involved), maintenance labours, number of persons carrying out the practices analysed [29], amount of energy invested in the management practices (distances travelled, hours of labour, amount of fuel used), type of tools (from sticks and stones to simple tools to machines with different complexity), management strategies (management plans, from individual to collective agreements, regulations), occurrence of artificial selection (from the recognition of varieties of a species to their differential use and management, and the degree of intensity or systematic selection) and the amount of products obtained per area, among other parameters [17, 25].

Because the natural systems are affected by human activities and vice versa, it is necessary for an interdisciplinary and holistic approach for studying management. Biotic and abiotic resources are part of systems (ecosystems and socioecological systems) and they affect and are affected by other components and by natural and human-guided processes. Therefore, the understanding of particular forms of a species management is necessarily connected with the general view of how a human culture manage the landscape or territory where people live. An integral compre-

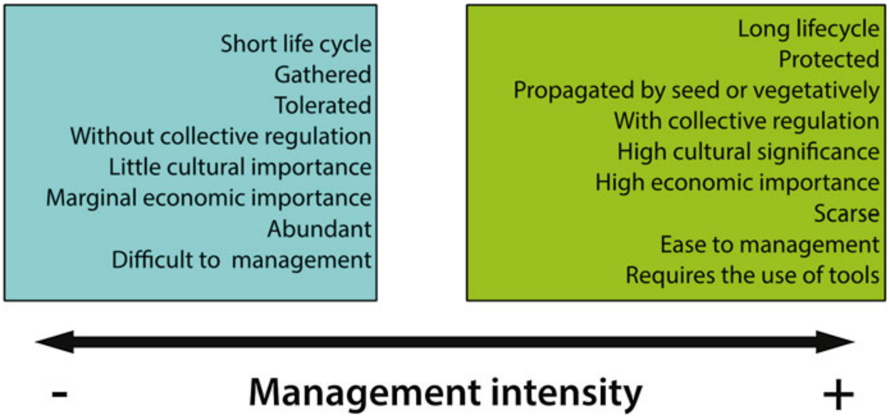

Fig. 10.12 General model explaining the relationship between ecological, sociocultural and technological with management intensity factors

hension of management systems which are complex systems is necessary for understanding the management and processes of innovation, as well as for developing appropriate innovation of technology for facing uncertainty and for constructing sustainable management of resources and socioecological systems.

The general model of Fig. 10.12 explains hypothetically how the different factors motive management and their relation with the intensification. Higher values of management intensity are expected in long life cycle species, with high cultural and economic importance, with relatively easy propagation requiring use of tools and whose use involves collective regulations. For the contrary, plant species with low management intensity are expected to be short life cycle species under simple gathering, with low cultural and economic value and without collective regulations for their extractions. These extremes of conditions allow supposing a continual gradient of states of ecological and cultural and economic value and management techniques that would represent the state of management intensity.

Relation Between Management Intensity and Uncertainty: The Case Study

In order to analyse how much the management intensity is a response to conditions of uncertainty in the availability of resources we examined the management and uncertainty associated to risk or vulnerability of a group of 33 edible plant species in Nahua communities of the Sierra Negra (Fig. 10.13). In this study we estimated the index of management intensity an index of risk based on a set of ecological, sociocultural and technological variables [17]. For each species the value of the risk index was a multivariate factor calculated as the first component of a PCA of all the indicators considered. The values were standardized in a scale from 0 to 1, in which

1 was the value of maximum risk [17]. Similarly, the management intensity index was the first principal component of all the variables and indicator considered in the evaluation of management intensity [17]. A regression analysis between management intensity and risk values allowed identifying a highly significant relation; in other words, the highest values of management intensity were found in plants with higher risk. A canonical correlation analysis indicated that variables that mainly influence risk are ecological variables (mainly distribution and abundance) as well as some sociocultural variables (mainly number of uses and economic value in markets). These results indicate that rare, scarce species with high cultural importance with commercialization have the highest risk and are under management practices, more intensely managed than other plant species that are abundant, with low cultural importance and no commercialization.

All the information referred to above suggests that at least in the case of edible plants the management is strongly related with the interest in decrease risk in availability of food. This scheme of analysis could be true also for medicinal plants and probably others used as fuel. In the first case because people look for having their availability ensured and close enough for attending health emergencies. In the second case because fuel wood is a continual worry in the daily life and people perceive a progressive scarcity of secure sources to satisfy their needs. Both groups of resources are for instance well represented in homegardens and other agroforestry systems where people indicate those purposes as motives to maintain plant species within those management systems. However, both management and domestication of plants appear to be more complex issues. Humans are not subjects acting as cause-effect responses and their culture is commonly much more than responses to this type of situations. Creativity and continual experimentation are parts of human nature. Scarcity and availability uncertainty is difficultly a main motive for cultivating ornamental plants, for instance. In that case are beauty and spiritual well-being more important than scarcity or uncertainty. This and other similar issues are still to be investigated.

Theoretical and Practical Implications of Studying Motives of Management

Understanding the way through which people construct their management strategies is highly important to understand causes and factors that led to the origins of agriculture and domestication of plants and animals. At the same time, the studies of present processes indicate that such motivations are alive, not were an issue of past times.

In addition to the theoretical relevance, the study of motives of management among indigenous communities may help to reconstruct an inventory of human experiences for managing resources and ecosystems. The desirable sustainable management difficultly is yet to be invented. For the contrary, sustainable strategies should be constructed upon the bases of the human experience worldwide. Mexico

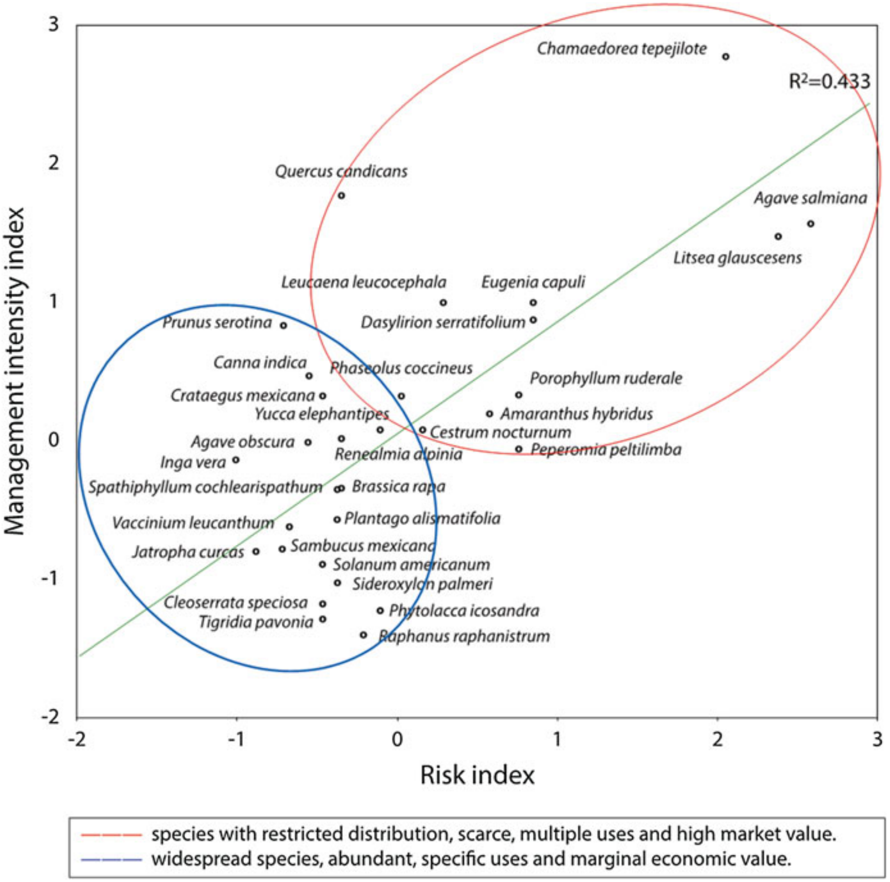

Fig. 10.13 Regression analysis between the management intensity index depending of risk index, calculated as the scores of the first principal component of a PCA in 33 edible species in the Sierra Negra, Mexico ($R^2=0.433$, $p<0.001$)

is a privileged setting of the world combining a high diversity of ecosystems, biological diversity and richness of human cultures. All these conditions offer a valuable opportunity to develop new strategies of sustainable management combining the local experience and orienting science to increase the potential of such experience. Ethnobotanical and ethnobiological approaches have therefore an important role in putting together the two perspectives in order to achieve vigorous innovative management strategies.

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Chapter 11
Evolutionary Ethnobotanical Studies of Incipient Domestication of Plants in Mesoamerica

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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

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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 leaded 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 km^2 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 biocultural 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 disfavouring 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 vale 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 that 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].

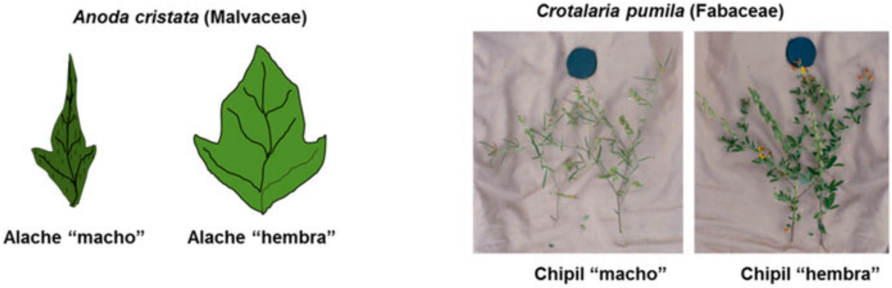
As discussed more deeply in the chapters by Blancas et al. and Casas et al. (Chapters 10 and 8 in this book, respectively), among these practices we include the tolerance, which occurs when people clear the forest and leave standing some species and particular phenotypes of those species; induction, 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.

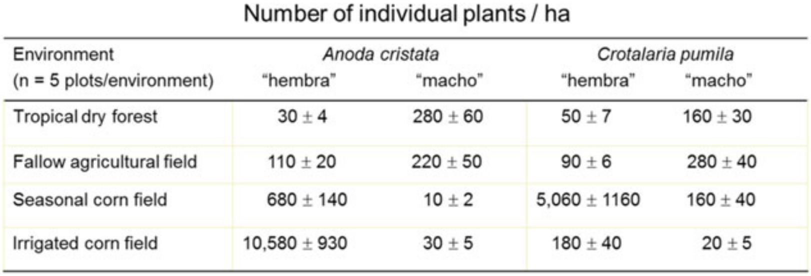
Through domestication, human beings manage genetic variations or genetic resources mainly through artificial selection, but also through other evolutionary forces such as breeding systems, gene flow, and genetic drift. The mechanisms and criteria guiding domestication are deeply linked to human culture; 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





Number of individual plants / ha

Environment (n = 5 plots/environment)	*Anoda cristata* “hembra”	 “macho”	*Crotalaria pumila* “hembra”	 “macho”
Tropical dry forest	30 ± 4	280 ± 60	50 ± 7	160 ± 30
Fallow agricultural field	110 ± 20	220 ± 50	90 ± 6	280 ± 40
Seasonal corn field	680 ± 140	10 ± 2	5,060 ± 1160	160 ± 40
Irrigated corn field	10,580 ± 930	30 ± 5	180 ± 40	20 ± 5

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 m^2 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 teneztli***” 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 teneztli***” 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.

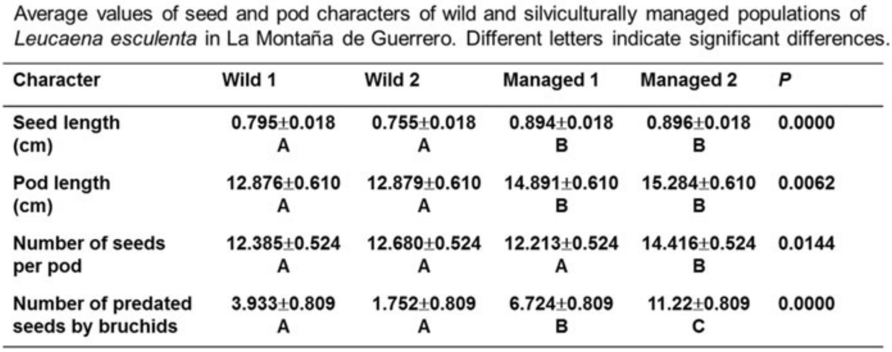
Other attributes may also be significant in quelites perception, use, and management. For instance, Blancas et al. [7] found that in *Spathiphyllum cochlearispathum* (Liebm.) Engl. people recognize two varieties: (a) ***“elotlxóchitl”*** or ***“oloxóchitl”***, which produces green inflorescences with 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 mexiana*, 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-


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

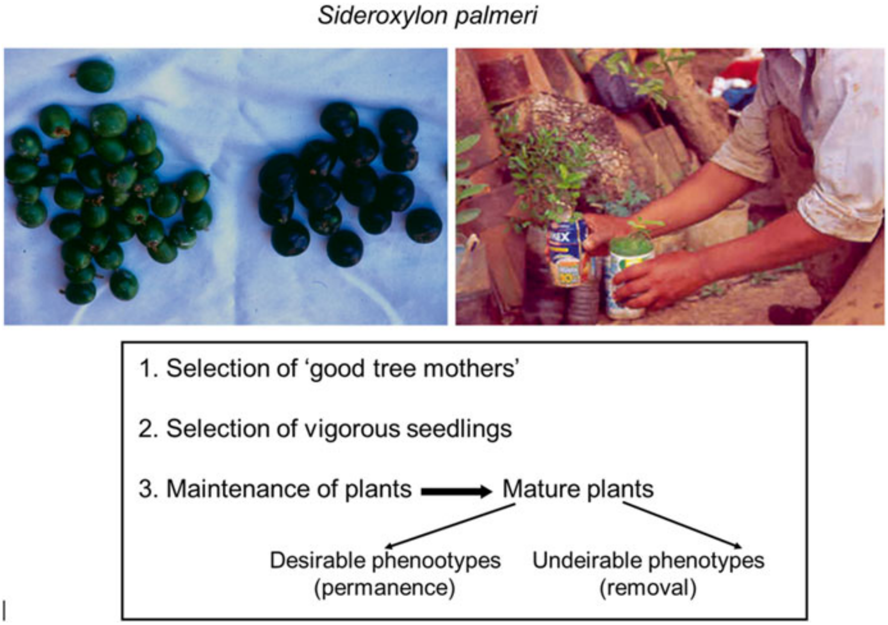


Fig. 11.3 The tempesquiste *Sideroxylon palmeri*. *Left*: aspect of immature and mature fruits. *Right*: aspect of young plants propagated from seeds in pots. *Bottom*: general scheme of artificial selection practiced in favour of plants producing larger spherical fruits with lower amount of latex. In 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 tempesquistle 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 prehistoric 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

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*

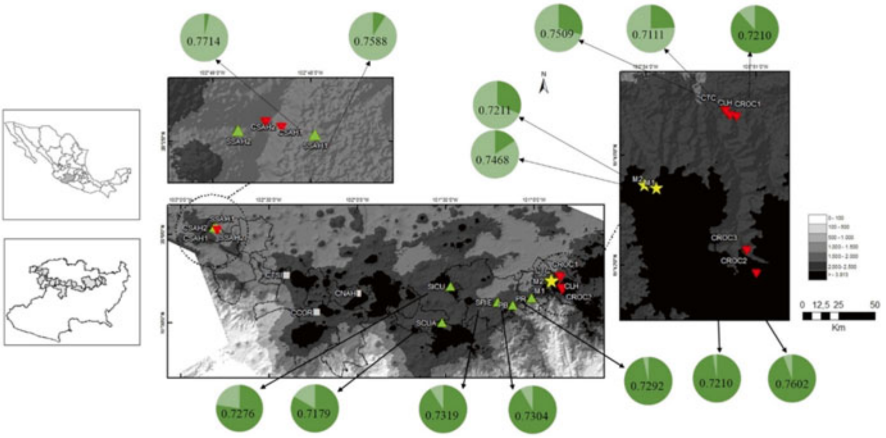


Fig. 11.5 Localization of the population of *Agave inaequidens* (*green upward triangle*) wild; (*red downward triangle*) cultivated; (*star*) managed y *A. hookeri* (*square*) studied in Central Occidental Mexico. Pie charts showing proportion of ancestry assigned to individuals of each population by 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 'maguey bruto' or 'maguey alto'. The escapes or 'quiotes' 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 'maguey grande' and small or 'maguey chico'), colour (green or 'verde', light green or 'cenizo', and dark green or 'negro'), form and size of leaves (wide or 'maguey de hoja ancha' and narrow or 'maguey de hoja estrecha'), and according to their use ('maguey bruto mezcal' and 'maguey 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

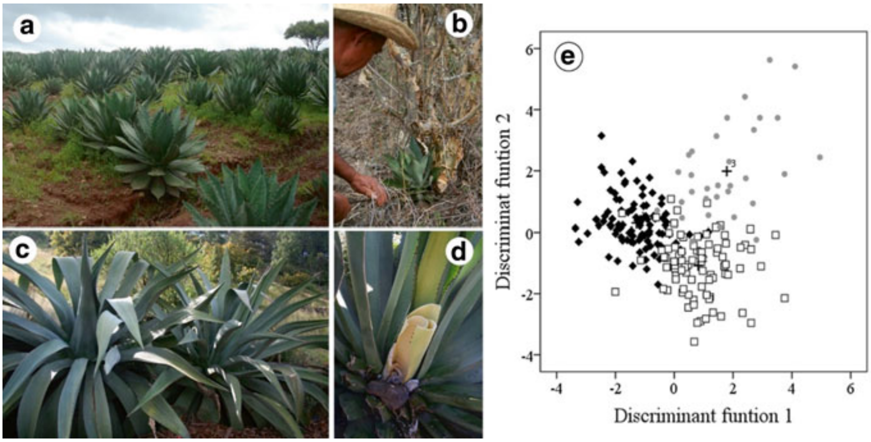


Fig. 11.6 (**a**) Cultivated population of *A. inaequidens*, (**b**) Collection of wild individuals for cultivation, (**c**) Individuals of *A. hookeri* in live fence, (**d**) Hollow in central cormo of *A. hookeri* to the collection of "agua miel", (**e**) Classification of *Agave inaequidens* individual 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 'jiotilla' (*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 'jiotilla'. The cultivation

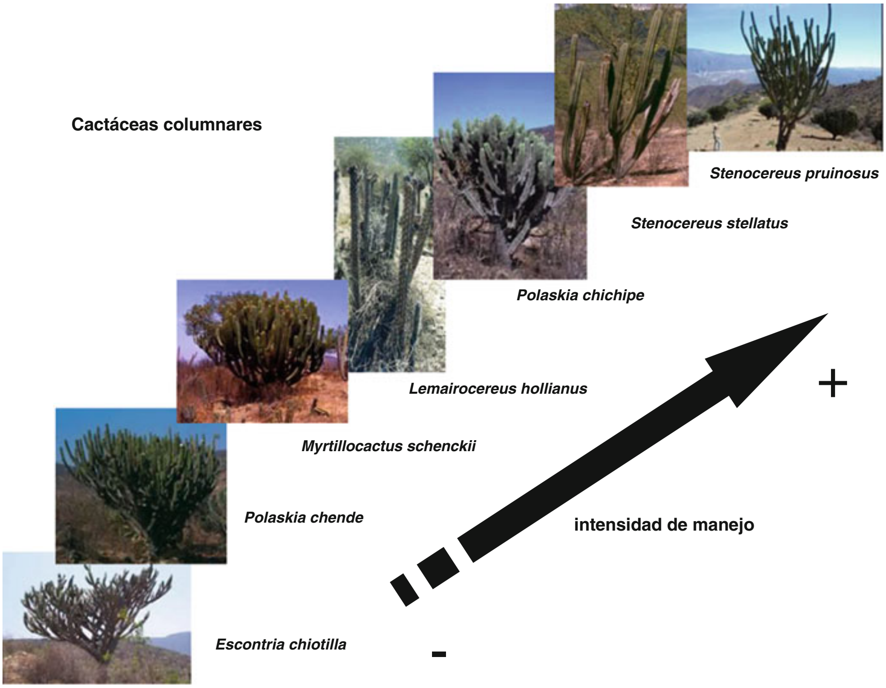


Fig. 11.7 Species of columnar cacti studied by our research team. We indicate the level of management intensity through the *ascendent arrow*, which was defined according to growth rate, viability of management associated to the possibility of vegetative propagation, and the intensity of artificial selection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

Ehnobotanical 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 chichipe* 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 Cóyotl et al. [57] documented that homegardens of cultivated populations of *Stenocereus* have much higher density of flowers than wild populations and are

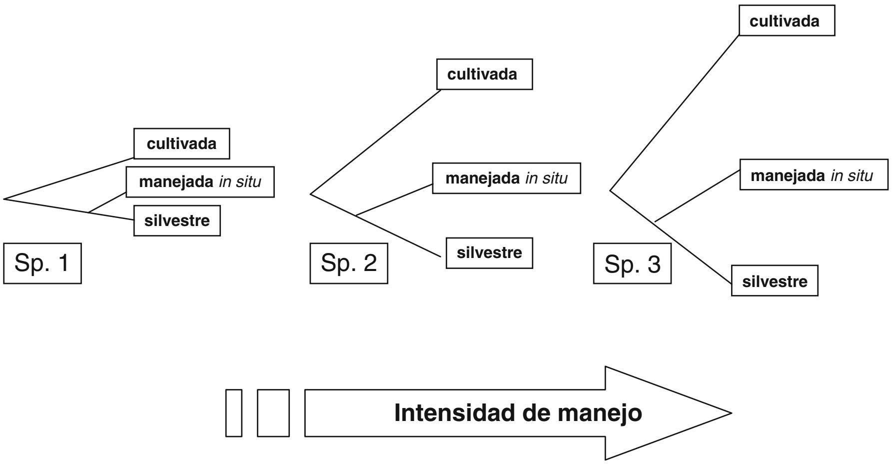


Fig. 11.8 Divergence in morphological, physiological, and genetic aspects expected between wild, silviculturally managed (in situ managed), and cultivated populations within and among species within a gradient of management intensity

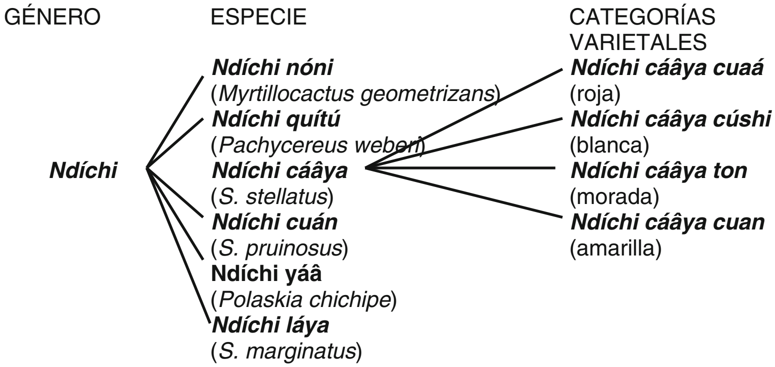


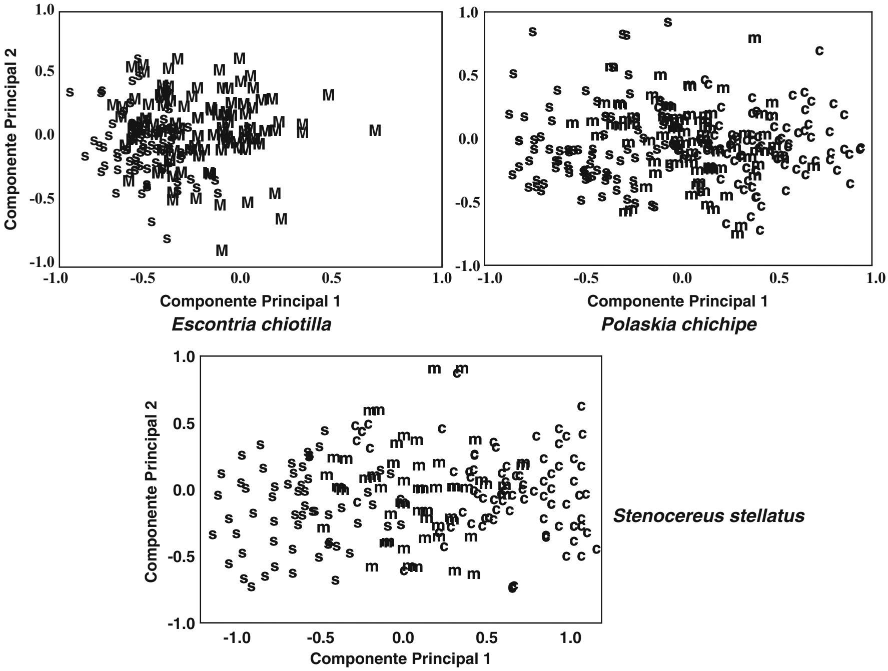
Fig. 11.9 Example of traditional perception of variation of columnar cacti. Mixtec classification of some columnar cacti species. All species of the group are classified through the term ***ndíchi*** which makes reference to the edible fruit of cacti. The name ***ndíchi*** is accompanied with and adjective 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 disturbation 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).



Escontria chiotilla

Polaskia chichipe

Stenocereus stellatus

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 columnar cacti

Especie	diferenciación entre poblaciones silvestres y silvícolas	diferenciación entre poblaciones silvestres y cultivadas
Polaskia chende	0.009	–
Escontria chiotilla	0.011	–
Myrtillocactus schenckii	0.069	0.110
Polaskia chichipe	0.193	0.353
Stenocereus stellatus	0.251	0.379
Stenocereus pruinosus	?	?
→ Management intensity		

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

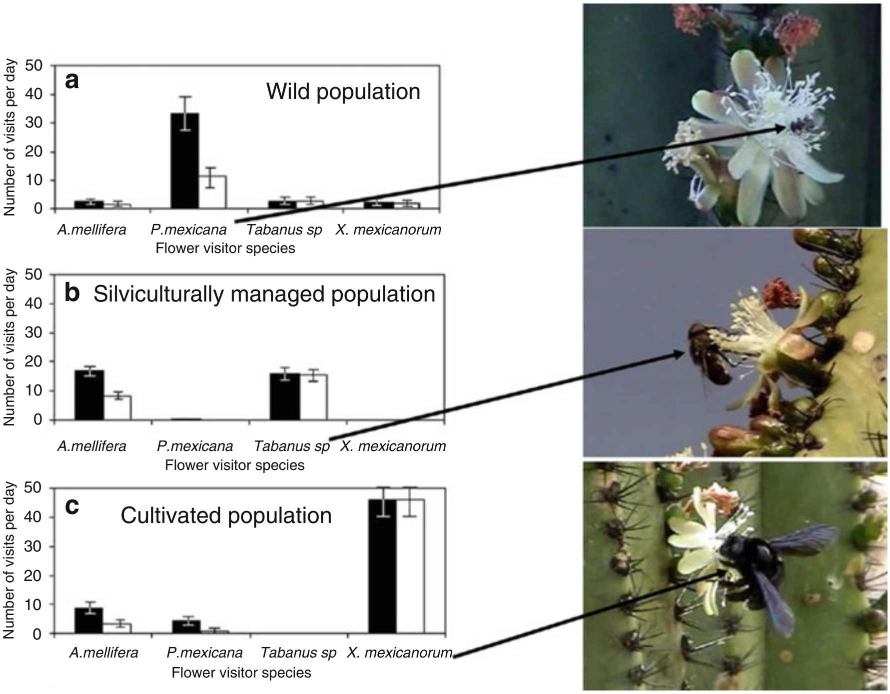
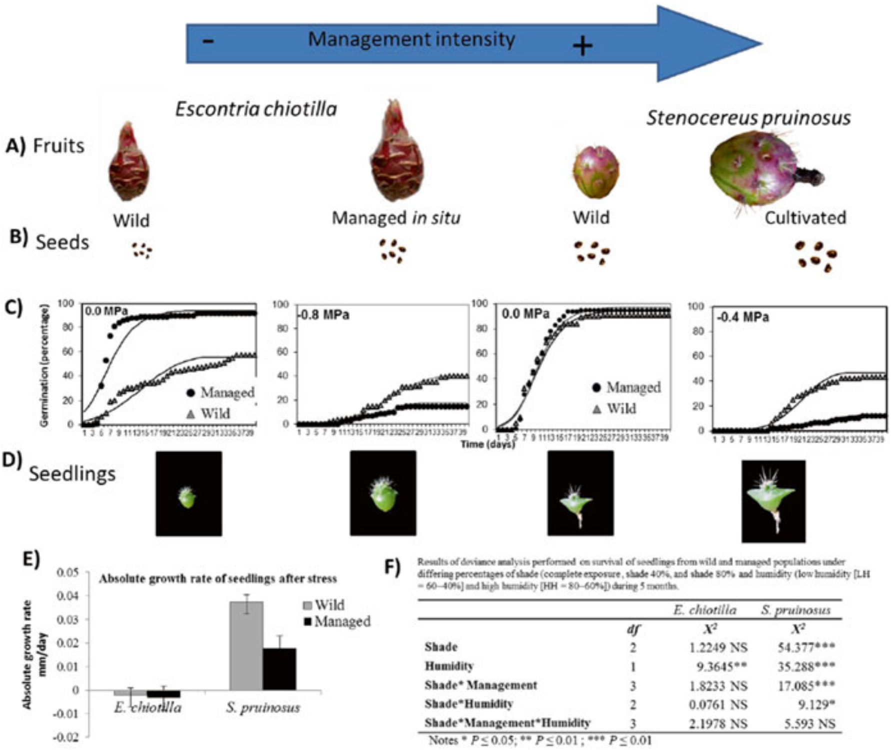


Fig. 11.12 General aspect of differential frequency visits to flowers of *Myrtillocactus schenckii* by meliponini bees (*Plebeia mexicana*) in wild populations, Tabanus sp. in silviculturally managed populations, and *Xylocopa mexicanorum* in cultivated populations. The differences in visit rates allows 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



Results of deviance analysis performed on survival of seedlings from wild and managed populations under differing percentages of shade (complete exposure, shade 40%, and shade 80% and humidity (low humidity [LH = 60–40%] and high humidity [HH = 80–60%]) during 5 months.

		E. chiotilla	*S. pruinosus*
	df	X^2	X^2
Shade	2	1.2249 NS	54.377***
Humidity	1	9.3645**	35.288***
Shade* Management	3	1.8233 NS	17.085***
Shade*Humidity	2	0.0761 NS	9.129*
Shade*Management*Humidity	3	2.1978 NS	5.593 NS

Notes * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.01$

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 I 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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Chapter 12
Ethnobotany of Mexican Weeds

Heike Vibrans

Abstract This chapter gives an overview of the relationship of people and weeds in Mexico. Weeds are understood as plants that are successful in human-disturbed habitats. It discusses origin and ecology, and focusses on their role in the traditional agricultural system and as useful plants. Mexican weeds are different because of their long relationship with humans, and the large stature of the main crop, maize. The maize field plays the role of the vegetable garden, with weedy species as vegetables at various levels of management. Many species exhibit improved traits as the result of in situ selection. Most edible wild-growing plants are products of maize fields, that is, agrestal species, while the largest number and most used medicinal plants grow in ruderal habitats. The importance of distinguishing agrestal from ruderal species in ethnobotanical studies is highlighted. The literature frequently emphasizes the role of weeds as a germplasm reserve, particularly the weedy relatives of domesticated crops. However, their economic role as part of production and risk-reduction strategy of farmers is rarely addressed with quantitative data. Several examples from small-scale studies document the considerable contribution of weedy species to the overall production of the system. The role of useful weeds for farmers and for society in general is discussed. A perspectives section analyzes which subjects are relatively well documented and those requiring more attention.

"… the impact of man upon his plants is not restricted to the relatively reduced number of present-day crops that constitute the bulk of human food sources, but may have had a very important expression in the multitude of accompanying species (usually maligned by the term "weeds" by Western agronomic culture) … by understanding these processes one not only learns about the ecological principles involved but also (and very importantly) about the purposes and the mental processes of the people who carved these evolutionary pathways for their benefit." (José Sarukhan, 1985) [1]

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Introduction

This contribution surveys general aspects of the relationship between people and weeds in Mexico as part of agricultural productivity and diversity, from both an ecological and economic point of view [1]. It does not focus on weed competition or control. Some subjects that have attracted much attention in the last decades, such as in situ selection and incipient domestication, are treated in more depth in other parts of this volume.

First, the meaning of the word "weed" in a Mexican/Mesoamerican context is discussed. Numbers are treated briefly. Then, we ask why Mesoamerican weeds are different, and why they are important. The role of weeds as a product in various parts of the agricultural production system is examined and an overview of different uses given. Finally, the economic role of these plants is analyzed in some detail. In several sections, I make suggestions on how the idiosyncrasy of the Mesoamerican agricultural system may have influenced cultural traits of present-day Mexicans and which topics are still under-researched.

What Are Weeds?

Weeds are creatures of humans. Most are plants that have adapted to human ways and habitats just as much as cultivated and domesticated plants have. Many species or biotypes could not survive without the habitats created by *Homo*. This adaptation involves changes in physiology, germination, growth parameters, and morphology, in a way similar to how domestication syndromes develop in domesticated plants [2–4]. But, while the forces acting on weed evolution are largely man-made, selection pressures on weeds are (mostly) undirected by human purpose, in contrast with domesticated plants; some exceptions are mentioned below. However, they certainly fall under the purview of ethnobotany as the study of the relationships between plants and humans.

There are many definitions of weeds, such as unwanted plants or pioneers. For our purpose the most appropriate definition of weeds is one used by Baker [2] and Rzedowski [5] Chap. 4: they are vascular plants that grow, reproduce, and disperse in habitats strongly modified by human beings, without direct help from humans. However, even this very general definition is not always completely accurate, as we will see further on.

It should be noted that Mesoamerican farmers generally do not have a word for weed in an agronomic sense. Mestizo farmers generally refer to the wild plants growing in fields as *hierbas*, herbs, while *jehuite* is a nahuatl-derived word for herbs that are useless. Wild vegetation outside of fields is often called *monte*, without differentiation. Neither of the words implies a value judgment (but also see the nomenclature reported by Chacón and Gliessman [6]). Indigenous languages have their

Fig. 12.1 Weeds in a Mexican highland maize field. The dominant species are *Cosmos bipinnatus* Cav., *Bidens odorata* Cav., *Tithonia tubiformis (Jacq.) Cass.*, and *Simsia amplexicaulis (Cav.) Pers.*

own nomenclature, but the terms related to "weed" generally do not have negative connotations.

Weed species and communities are not homogeneous entities [4]. There are many kinds of disturbance by humans, and plants are selected by type of disturbance. Simple observations show that a sand heap left from construction will be colonized by short-lived species with wind-dispersed propagules. The cracks in a sidewalk will have plants that have strong, deep primary roots and can resist trampling. A rubbish heap will often be covered by resistant cultivated plants that germinated or grew from garden refuse. A roadside is generally dominated by grasses that resist mowing. A rubber or coffee plantation has plants that can grow in the shade. An apple or grape plantation will often have some geophytes that flower early, before the canopy closes. A rye field harbors species that can germinate at low temperatures, just like the main crop. Maize and other row crops have plants that can produce several waves (cohorts) of growth, as the early emergers will be weeded out. And, of course, they are all influenced by soil, climate, intra- and interspecific competition and other biotic and abiotic factors, just like all other plants.

However, we can distinguish two main types of terrestrial weeds (aquatic and silvicultural weeds are not treated here). One type is agrestal weeds that grow in tilled soil (Fig. 12.1). The plants are frequently subject to attempts at eradication, but the soils, nutrient regime, and water status are generally conductive to plant growth and relatively uniform. The disturbance regime is severe, but cyclical and regular [3, 4].

The other type is ruderal plants. These also grow in disturbed places. However, the disturbance is mostly irregular, and only occasionally involves soil movement. These are often sites associated with human settlements: surroundings of houses and farms, garbage heaps, sports fields, parks and gardens, sidewalks, walls, or communication connections (road and railroad margins, rights of way), or the edges of fields and irrigation channels. Plantations, pastures, and some other crops cultivated without tilled soil can also be included in this group. The main disturbance types include mowing, trampling, selective weeding, some general eradication, or difficult growing conditions (drought, poor and meager soils, lack of nutrients).

These differences in environmental conditions strongly influence the ecology. Agrestal weeds are generally annuals or perennials with good capacity for resprouting from segments and for adapting to the crop. Ruderal plants are much more likely to be perennials [4]. Both are selected for and adapt their pollination and dispersal strategies to those media available in their habitat, which may vary considerably.

Many species of weeds have their origin in naturally disturbed vegetation (riversides, burned or storm damaged sites, clearings, sites disturbed by animals); some derive from natural vegetation, for example, desert annuals [7]. In addition to developing biotypes from the variation present in wild populations, some have broadened their genetic base and evolved new or strongly modified taxa through hybridization with relatives, introgression, polyploidy, and selection, just as domesticated species have [2, 7]. People have selected biotypes both negatively (weeding) and positively (tolerance and encouragement of useful forms). Thus, the limit between weed and cultivated/domesticated plant is not always clear.

How Many Weeds Are There in Mexico?

As in other regions of the world, in Mexico about 10–12 % of the flora can be called weedy. As the country has a very rich and diverse flora, its weed flora is also one of the richest in the world—about 3000 species [5, 8, 9]. If species of the general secondary vegetation flora, particularly of secondary forests, are counted, the number is probably much higher. Gómez-Pompa [10] stated that the diversity of many taxa of the tropical flora cannot be properly understood and analyzed without considering their role in secondary vegetation. Preadaptation may have occurred because of the numerous natural forces in the area that cause disturbances in the natural vegetation, such as flooding and hurricanes.

Direct human influence should not be discounted in preadaptations. Humans have been a strong influence on vegetation since the end of the last ice age [11]—through management, fire, influences on the populations of herbivores, and soon afterwards, swidden and permanent agriculture. The vegetation of Mesoamerica, like that of the Mediterranean and some Far Eastern landscapes, has been profoundly shaped by humans. Areas that are really wild, that is with no human influence, probably exist only in some very inaccessible sites. Bye y Linares [12] provide an impressive list of the ways people have influenced their surrounding vegetation and taxa in Mexico.

A remarkable fact about the Mexican weed flora is the relatively low number of introduced plants—somewhat over 600 species, and less than 3 % of the flora [9, 13, 14]. Mexico shares this low proportion with some other regions that are believed to be regions of agricultural origin, such as Israel, China, and Java.

In Mexico, as in other parts of the neotropics [15], the worst terrestrial invasive species are African tropical grasses, which were introduced for and are promoted by cattle, sheep, and goat ranching, a completely new disturbance type for the New World. In contrast, introduced agricultural weeds such as *Brassica rapa* L., *Malva parviflora* L., *Reseda luteola* L., or *Raphanus raphanistrum* L. while common, appear to have integrated into existing systems, and are not particularly invasive in the sense of displacing native vegetation. A very large proportion of these introduced weeds are useful.

So, the relatively low proportion of invasive species in Mexico may be related to the long history of agriculture, in which local weeds were able to acquire a comparative advantage. If disturbance types change, species that evolved with these disturbance types (such as the large mammals of Africa) will be more successful.

Why Are Mexican Weeds Different?

As in the Near Eastern and Asiatic center of origin of agriculture, weeds in Mexico have a long history of coevolution with human disturbance, particularly agriculture [13, 14], and have developed specialized traits. However, they developed from a different biological and cultural matrix. Mexican weeds are different from most Old World agrestals and ruderals because of (a) the stature of the main crop (Fig. 12.2), (b) the almost complete absence of domesticated animals historically, and (c) the different ecological origin of the crops.

In the Near and Far Eastern centers of agricultural origin, small-statured grains dominate. It is not possible to walk around in the main crop for intercropping or other purposes. The exception are some large millets in Africa, and their effect on the weed flora is still to be explored. The intercropping of maize was adopted, presumably independently, in other regions of the world where maize was introduced. African farmers combine maize with their own cucurbits (or the Mesoamerican ones), with *Vigna* beans and with the equivalent of *quelites* (wild edible herbs) [16]. The same occurs in China (Fig. 12.3).

Another consequence of the large stature of maize is the ecology of its weeds. In Mexico, the dominant weed species are also large statured, with attractive flowers pollinated by insects and sometimes birds. Of course, there are also smaller species, but they have to be shade tolerant. Their diaspores are dispersed outside of the field by large (humans) and small mammals [17], depending on the size of the plants, and birds. Wind pollination or dispersal is not very successful in maize fields.

Fig. 12.2 The robust stature of maize has led to the development of large weeds, here *Tithonia tubiformis*

In Near and Far Eastern small grain agriculture, crop rotations and the integration of animal husbandry were the most convenient way to restore soil fertility, at least once population pressure limited the more (human-) energy-efficient swidden or slash-and-burn agriculture. In Mesoamerican traditional agriculture, nitrogen has been a limiting factor, although the region has the advantage of naturally fertile soils. Intercropped beans, of course, fix nitrogen. But the requirements of fertility maintenance has led to a system that is very common even today, of permanent plots on fertile soils (that are enriched with whatever biological material is at hand) and satellite plots that are cultivated only periodically. In areas with poor soils, highly regimented swidden systems were maintained even when populations became relatively dense, until the advent of chemical fertilizer [18]. Domestic animals were adopted rapidly, partly because they are manure producers and can transfer nutrients from the natural vegetation the fields.

Most Mexican crops derive from wild plants that grow in the western part of south-central Mexico, that is, the Balsas river basin and adjacent regions to the north. Casual observations indicate that many maize weeds may have the same ecological origin, but there are no studies on the subject. The following table compares some ecological characteristics of domesticated plants in Mesoamerica and the Near East/Europe, identified by Iltis [19] that also appear to apply to Mesoamerican weeds, based on preliminary observations and a few case studies (Table 12.1).

Fig. 12.3 In regions where maize was adopted as a main crop, people developed mixed cropping patterns similar to the Mesoamerican milpa. This maize field with intercropped *Vigna unguiculata* (L.) Walp.was found in southern China

Table 12.1 Comparison of characteristics of Near Eastern and Mesoamerican crops based on Iltis [19], that also appear to apply to their weeds

Near East (cereals and legumes)	Mesoamerica (maize, beans, and squash)
Derived from annual wild species	Derived from annual and short-lived perennial wild species
Autogamous; in Israel and the Fertile Crescent about 50 % of the annual species are autogamous	Allogamous; although there is no data on the proportion of autogamous species in Mesoamerica, it is probably lower than in the Old World ecosystems
Long-day plants	Short-day plants
Winter germination	Summer germination
Maturing in spring and early summer	Maturing in fall
Adapted to cool temperatures	Adapted to subtropical temperatures
Small, slender plants	Large plants (at least the dominant species)
Wild species form massive populations in the ecotone between deserts and temperate forests	Wild species form dispersed populations

Management of Useful Weeds

Most weedy plants in Mexico, particularly agrestals, are useful in one way or the other, and a large proportion are multipurpose [20, 21]. Milpas (maize fields with or without intercrops) tend to have more useful weeds than other crops [21]. While farmers appreciate the contributions of weeds, they recognize that weeds compete with their crops. They also consider some plants noxious because they hinder agricultural practices, such as viny, spiny or stinging species [17, 20, 21], or because they are toxic. They are also aware that some species are more noxious than others [6, 21].

Normal agricultural practices lessen the competitive capacity of weeds and truly unwanted plants are eliminated individually if possible. However, once the critical period of the crop is over and weed growth has less influence on the yield, the spontaneous vegetation is left to grow freely. If it is controlled, it is to make harvesting easier.

Useful agrestal weeds are the focus of a whole scale of management practices that go from none through tolerance, encouragement, selection of best types, to management that is practically cultivation on the road to domestication. Management includes activities such as sparing plants during weeding, leaving a few individuals to seed, or introducing a few seeds if the plant was not yet present. Blanckaert et al. [21] found that 1/3 of the non-forage species were managed in some way.

Incipient domestication or in situ selection have received much scientific interest, since a seminal paper by Robert Bye described incipient domestication of mustards in the Tarahumara Mountains [22]. These processes include both annual plants (mostly weedy agrestals) and various useful perennials. Casas et al. [23] provide useful, general overviews; Blanckaert et al. [24] review the literature focusing on weeds.

Examples of weed taxa studied for the effects of the management and in situ selection include *Lycianthes moziniana* (Dunal) Bitter [25], *Amaranthus* [26, 27], *Anoda cristata* (L.) Schltdl. [28, 29], *Melothria pendula* L. [30], *Jaltomata procumbens* (Cav.) J. L. Gentry [31], and *Chenopodium (Dysphania) ambrosioides* L. [24].

Management intensity is often dependent both on individual idiosyncracy—not all farmers manage weeds differentially [21]—and on land tenure. For example, short-lived plants are apparently managed more intensively on private land [32]. Markets and market access also play a large role, as do considerations of risk, and the relationship of availability and demand [20, 33].

The fact that many of these useful plants depend on some amount of human management is not only shown by differentiated biotypes, but also by what happens if management ceases. A recent, unpublished study by Cristóbal Sánchez on the weed vegetation of San Juan Ixtenco, a community in the state of Tlaxcala, found that many of the edible plants (e.g., *Jaltomata procumbens* and *Chenopodium berlandieri* Moq.) have practically vanished from the fields, though people still remember them well. This is mainly due to the changes in agricultural practices and in the social situation over the last 10–20 years: increased mechanization does not allow concurrent collection of weedy quelites, herbicides affect dicots more, and people's time is worth more, as almost everybody has other sources of income, so that collecting and preparing food comes with a higher opportunity cost.

An interesting detail of the use of wild weeds is the fact that in several cases we registered a gender conflict on weed management. Understandably, male farmers tend to want to make their work easier, particularly the hard physical work of weeding; once herbicides are cheap enough, relative to their time value, they are often happy to apply them. Women, on the other hand, wish to be able to collect quelites and medicinal plants for the family's meals and health care. They try to get their husbands to leave at least some areas untreated, but they are not always successful [16, 34, 35].

In this context it is significant that, of the small number of useful plants that were exchanged between the New and the Old World before the Columbian voyage, two are weedy, agrestal quelites. *Sinapis arvensis* L. (=*Brassica kaber*) was found in archeological contexts in the eastern USA [36], and *Portulaca oleracea* L. was relatively abundant in several excavations in central Mexico [37].

The Spatial Components of the Traditional Mexican Agricultural System and Their Weeds

The Mesoamerican agricultural system consists of several, relatively well-defined and ecologically distinct components. There are, of course, the cultivated fields and home gardens. However, the field margins and ruderal habitats are also part of the productive system, as are oldfields, secondary and primary forests, and aquatic environments. The following sections deal with fields, home gardens, and field margins.

The Cultivated Fields

A crucial difference between maize and small grains as main crops is the fact that one can walk around in a maize field without damaging the main crop, which is not possible in small grain fields, particularly those sown (originally) broadcast, as was mentioned above. This has an important consequence. In Europe and the Far East, the impossibility of walking in the fields meant that other annual crops needed in smaller quantities had to be cultivated separately, that is, in vegetable gardens. In Mexico, the milpa is also the vegetable garden; this observation has been made repeatedly [38, 39], but has apparently never entered popular consciousness, particularly that of Western-trained agronomists, in detriment of appropriate agricultural policy.

However, the plants in the milpa are not under supervision as they are in a fenced garden. People and animals can help themselves to whatever grows there, and therefore, farmers generally do not want to invest much additional effort in growing their vegetables in the milpa.

With this background, it is not surprising that the Mesoamerican vegetable complement of the food system consists mainly of spontaneously growing plants that

Fig. 12.4 Old World crops were adapted to the conditions of the milpa agriculture. A form similar to wild type *Brassica oleracea* is encouraged in Oaxaca and Chiapas. The left picture shows a semi-wild *Brassica oleracea* in a maize field in Oaxaca, and the right the same species as commercialized in the market of San Cristobal de las Casas, Chiapas

can maintain their populations autonomously, or with just a little help from the farmer, as discussed above.

Mesoamerican farmers even took some more or less wild or domesticated European plants and integrated them into this system. A relatively large number of the plants called quelites in Mexico are introduced, and are managed in the same way as the native species. Figure 12.4 shows some individuals of *Brassica oleracea* L. that resemble the wild type in a milpa in Chiapas; in the humid mountains of Veracruz and Oaxaca, another type of *Brassica oleracea* occurs in milpas, this one with white flowers. We do not know yet whether these types were introduced and adopted, or if they represent regressions from the domesticated forms.

Home Gardens

In home gardens the situation is similar to that in maize fields, but inverted. In Mexico, people grow few annual plants in their gardens. In addition to the planted perennial fruit, ornamental and medicinal plants, we find a complement of weedy perennial and hardy annual herbs, mostly medicinals and ornamentals that have to fend off the turkeys, chickens, pigs, and ducks with which they share the garden. However, they are appreciated and often managed if they appear [40–42]. Examples of annuals are *epazote* (*Chenopodium ambrosioides*), *cilantro* (*Coriandrum*), or *manzanilla* (*Matricaria*), and examples of perennials are *diente de león* (*Taraxacum* *officinale* F. H. Wigg.), *hierba maestra* (*Artemisia ludoviciana* Nutt.), and *asomiate* (*Barkleyanthus salicifolius* (Kunth) H. Rob. & Brettell). Here, too, it is often difficult to decide if a species is cultivated or weedy.

This tradition has policy implications. There have been numerous attempts to promote European-style home gardens with annual plants such as cabbage, tomatoes, carrots, and beets in Mexico, in order to improve nutrition of rural and urban households. Most of them have been unsuccessful or were adopted by only a few persons. I suggest that this is due to the lack of tradition, which leads to a lack of intimate knowledge of techniques such as sowing small-seeded crops in rows, thinning, timing of cultivation and appropriate spatial combinations. This contrasts with the fact that every rural female in Mexico is very adept at propagating perennial species, and *piecitos* (shoots) of both cultivated and wild-growing plants are commonly exchanged and given as gifts during visits.

There is an interesting exception to the general rule that milpas intercrop plants consumed as vegetables, and home gardens perennial plants. In Yucatán, in the Maya region, home gardens often have a fenced section planted with annuals and geophytes, such as lettuce, onions, and cabbage; they often have raised seedbeds called *ka'anche*. Also, milpas may include a maize-free zone, the *pach pakal*, where other vegetables such as cabbage are cultivated. After seeing similar structures in China, I suggest that these were adopted from the Chinese population that arrived in Yucatán during the henequen fiber boom in the nineteenth century. However, this has to be explored further, probably through historical documents.

In general, Mexicans have a strong tendency not to let any useful plant part go to waste. If a geranium branch breaks, it is stuck in soil somewhere else, *a ver si pega* (to see if it "sticks") or is given as a gift; if a tomato plant germinates, even if it is between the flowers, it is tolerated. I consider this a result of the way gardens and vegetation are managed traditionally.

Field Margins and Ruderal Habitats

Field margins and their vegetation are part of the Mesoamerican agricultural system. They serve ecological purposes, for example, to detain erosion, social purposes, to separate holdings as fences and hedges, and also have a productive function. Here, many less valuable perennial plants are cultivated, encouraged, or tolerated. These may include fruit trees, *Agave*, various cacti, trees for firewood, and numerous medicinal, ornamental, edible, or forage herbs. Almost all of them can propagate by themselves (though they are occasionally planted or transplanted); that is, they are weedy. The production of these components may be highly relevant economically, but they have been studied little [43, 44]; an example of their economic relevance is given in the section on economics.

Once fields are mechanized, these components become an annoyance and are often eliminated. Invasive plants, for example, the kikuyo grass (*Pennisetum (Cenchrus) clandestinum* Hochst. ex Chiov.) have also been displacing the native, useful vegetation.

Wild Relatives of Cultivated Plants

Most wild relatives of the main annual or short-lived Mesoamerican domesticates, such as maize, various species of beans and cucurbits, tomato (Fig. 12.5), chili, tomatillo, and cotton, are weedy. They are often used in various ways, sometimes similarly and often differently from the domesticated forms [30, 45].

These wild populations frequently grow near the domesticated plants and introgression has been shown for various crops [46], for example, for maize [47], *Phaseolus* beans [48], and *Cucurbita fraterna-Cucurbita pepo* [49]. Understanding the relationships between domesticated plants, their nearest weedy relatives and human activities has also become essential for many modern agricultural problems, such as herbicide resistance and the use of transgenic crops [49, 50]. Also, they are fast becoming the most serious and difficult-to-combat weeds, because of their similarity with the crop [51].

Weedy plants still originate cultivated species. An example is the use of teosinte for forage that has led to improved varieties. One of the numerous weedy *Physalis* species with edible fruit, *Physalis angulat*a L., has been taken into cultivation in Jalisco [52]. Figure 12.6 shows small plots where normally wild-growing species, *Crotalaria longirostrata* Hook. & Arn. and *Solanum americanum* Mill., are cultivated.

Fig. 12.5 Wild tomatoes in a maize field

Fig. 12.6 Weeds being cultivated. The *left* image shows the cultivation of *Crotalaria longirostrata*, and the *right* one *Solanum americanum*

Uses of Weeds

Weeds as Food

The focus of most studies on useful weeds has been on their role as food. This contribution only contains some general observations on the subject of wild edible plants, as other parts of this volume treat the subject, and an excellent overview was published recently [53].

Around the world, many weedy plants are used as food [54]. This is partly due to the growth strategy of many of the species, particularly of agrestals, that invest more in vegetative growth and less in defensive morphological structures and chemical compounds, in order to grow biomass rapidly and thus survive the intensive competition with the cultivated crop (r-type selection). Ruderal plants vary more, particularly with respect to chemical defense, as will be seen below.

In Mexico, plants used as green, spinach-type vegetables are known under the name of quelites. This is derived from a Nahua word, quilitl, which means edible herb and is often used as a suffix in plant names [55]. Examples are *papaloquelite* (*Porophyllum*), the “butterfly edible herb,” which has leaves that flutter in the wind, *ayotquilit* (*Cucurbita pepo* L.), derived from the nahua word for squash, *ayotli*, *totomoxquilit* (*Sonchus oleraceus* L.), allusive to the fact that it grows when the maize is dry (*totomoxtle* are dry maize bracts). It is also used in combination with Spanish-derived words such as *berrosquilit* (*Nasturtium officinale* W. T. Aiton, watercress), derived from the Spanish *berro* (examples from Molina-Martínez

[56]). These plants do not necessarily have to be weeds or even herbs. For example, the young leaves of *Leucaena esculenta* (Moc. & Sessé ex DC.) Benth. (*guaje*), a leguminous tree, are also considered a quelite.

Several of these species are well known from the archeological record, particularly *Amaranthus* and *Chenopodium*. Also, seed of *Portulaca oleracea*, *Oxalis*, *Chenopodium ambrosioides*, and *Suaeda* has been found repeatedly, and *chipil* (*Crotalaria* sp.), *jaltomate* (*Jaltomata*), and *chivitos* (*Calandrinia*) occasionally [37].

Wild plants considered quelites are numerous. But those that are most used are almost always weeds of cultivated fields, that is, agrestals. For example, of the 120 species of quelites known to the Tarahumara, only ten are used regularly, and they all grow in fields (*Amaranthus retroflexus* L.*, Chenopodium ambrosioides, C. berlandieri, Bidens odorata, Cosmos parviflorus* (Jacq.) Pers.*, Brassica rapa, Lepidium virginicum* L.*, Anoda cristata, Portulaca oleracea*, and *Urtica dioica* L.) [57]. This may be related to both the biological characteristics mentioned above and economics, particularly opportunity costs—it is more efficient to collect/harvest in a place where one goes anyway (fields) during activities that one does anyway (weeding).

Preparation of quelites is often simply frying with oil, onions, and salt. However, there are many other ways. Some are part of soups (*Amaranthus, Malva*), steamed or parboiled, or eaten fresh. Others are the main stuffing of tamales (chipil, two species of *Crotalaria*) (Fig. 12.7). *Portulaca* is part of a standard sauce used for cooked pork. Some species are cooked and the cooking water discarded before consumption, in order to reduce bitterness. Mota-Cruz et al. [58] reported fermentation of *Cleome* before consumption.

In the humid mountain regions of Veracruz, Oaxaca and Chiapas people consume several species of Solanaceae (Fig. 12.8), some of them thought to be toxic [58]. They often have to be treated before consumption, or their production managed, for example by coppicing, in order to lessen bitterness, and presumably, lower alkaloid content—this subject has not yet been studied.

Some other weeds are condiments rather than vegetables. Examples are the widely known *epazote* (*Chenopodium ambrosioides*), also an important vermifuge, *papaloquelite* (*Porophyllum macrocephalum* DC.), *hierba santa* (*Piper auritum* Kunth), and *lengua de vaca* (*Rumex obtusifolius* L.*, R. crispus* L.).

A few species are also used for the popular drinks, *aguas frescas*, for consumption with meals. For example, *Portulaca* can be combined with cucumber and lemon for a refreshing summer drink. The seed of *chia* (*Salvia hispanica* L.), a weed and cultivated plant, now widely promoted as a superfood and source of omega-3 fatty acids, is a popular modifier of the consistency of homemade lemonade.

Quelites—and food in general—are subject to the Mesoamerican hot-cold system, that believes that health is a balance between the two extremes and that several factors, again including food, can disturb this balance and cause illness [56, 59]. Quelites can have cold or hot properties and should not be consumed in an unbalanced way.

A few studies have tried to quantify quelite consumption [16, 20, 60, 61]. Not surprisingly, it varies strongly and is decreasing as people adopt a more urban lifestyle. Today, people even in remote areas eat quelites perhaps only once, or at

Fig. 12.7 Quelites are part of many dishes; this is a tamal with *chipil* (*Crotalaria* leaves)

Fig. 12.8 In the humid mountain areas, several species of the Solanaceae family are consumed as quelites. At the *left*, *Solanum nigrescens* Mart. & Gal.on sale in the south of Chiapas; to the *right*, a meal combining *Solanum americanum*, tomato, cheese and beans, in the Chimalapa, Oaxaca

most 2–3 times a week, whereas earlier workers reported practically daily consumption during the rainy season [57, 62]. One study showed that quelites significantly contribute iron, calcium, Vitamin B2, and riboflavin to the diet [56].

Quelites confront problems that are partly the same as for vegetables in general: people do not have time for cleaning and cooking. However, quelites also have a serious image problem: they are strongly associated with poverty, and people substitute them with other vegetables (or the cheeses, meats, and breads associated with higher status) for this reason [63]. This is not a new phenomenon, but part of the colonial heritage—there are sources from the sixteenth century disparaging this the part of the indigenous diet [56, 64]; even early ethnobotanists were not free of the idea (“Most of these verduras or “greens,” however, supply scant nutriment, serving principally as bulk in the diet” [38]). The idea that wild-growing herbs are inferior still turns up to this day in newspaper articles and other popular literature.

Fig. 12.9 Elevating the image of quelites: (**a**) gourmet cooking event with top chefs of Mexico City; (**b**) beef filet with *Malva*; (**c**) a salad with verdolaga (*Portulaca oleracea*), jicama and tortilla strips, both from the cooking event; (**d**) an omelette with *Agave* flowers at El Cardenal, an upscale Mexico City restaurant

A group at the Botanical Garden of the UNAM has been working to reverse this trend by promoting the use of quelites among the general public, and among restaurant chefs (Fig. 12.9a–c). They have also published recipe books [65–67]. Their efforts have had some amount of success, and in the last few years, the ingredients have been appearing in gourmet restaurants with contemporary cooking (Fig. 12.9d), and even in some chain restaurants.

Weeds as Medicinal Plants

John Stepp and Daniel Moerman [68, 69] showed that a very large proportion of known medicinal plants in a Tzeltal population in Chiapas, and in North America north of Mexico, and some other regions, are weedy, and not so much derived from tropical forests, contradicting some earlier publications. The authors consider various factors that may cause this relationship: one is convenience for the users—plants growing at a distance are not as useful to the sick. Another factor is biology: long-lived, K-selected species tend to defend against herbivory with large quantities of high molecular weight substances that are metabolically inactive, but less digestible for animals, such as tannins and lignins. Fast-growing, r-selected species prefer to use small, less costly, toxic molecules for defense, such as alkaloids or terpenoids.

In Mexico, it has been shown repeatedly that ruderal weeds are the most common source of medicinal plants (apart from those cultivated in home gardens), by quantity, frequency, and degree of knowledge [34, 59, 70–73] (Fig. 12.10). They are often perennials, such as *Artemisia ludoviciana*, *Waltheria americana* L., *Buddleia* spp., and *Heterotheca inuloides* Cass., and some introduced species that are cultivated or naturalized (*Mentha* spp., *Origanum*, *Matricaria*).

However, plants commercialized on a large scale are often trees and shrubs from dry tropical forests that also have many defense mechanisms [74]. So, some other, still unexplored effects and differences may exist in function of the general climate and vegetation types.

There are relatively few species of agrestals that are widely used medicinal plants; *Chenopodium ambrosioides* and *Datura stramonium* L. are examples. They are strongly selected against by farmers, at least in milpas that are also expected to produce animal feed (see the next section).

Weeds as Forage Plants

Whereas weeds as food and medicinal plants have been studied to some extent, their role as forage or fodder plants is not well understood, despite the fact that this use is—or used to be—the most relevant one in terms of number of species, quantity, and economic value; this applies not only to Mexico [20, 21, 44, 75], but also to other regions, such as Brazil [76].

It has been shown repeatedly that a number of maize field weeds are good-quality animal feed [75]. Among these plants are some of the most dominant. They considerably improve maize straw based animal diets [77–79] and, with a few exceptions, lack high quantities of anti-nutritional factors such as tannins or phenolic compounds [80, 81].

Weeds not only add value to farm products (milk and meat) but also to its energy resources (food for working animals [44, 78]). Recycling weed nutrients through domestic animals/manure is an important way to maintain soil fertility and to reduce nutrient lixiviation; as weeds often explore other soil strata than their associated crops, they may even increase nutrient availability (Fig. 12.11).

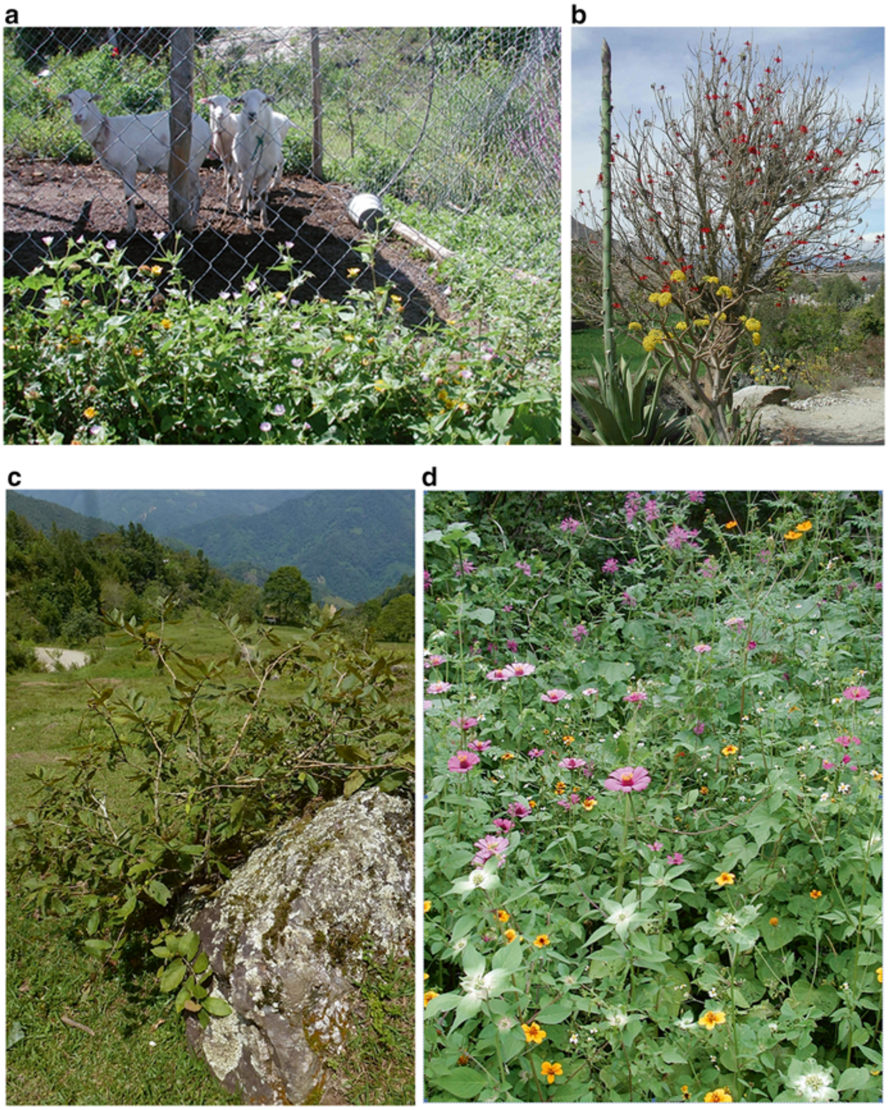

Fig. 12.10 Ruderal habitats are an important source of useful plants, particularly medicinals. (**a**) The plants in the foreground are *Anoda cristata*, a quelite, and *Grindelia inuloides Willd.*, a medicinal plant. (**b**) *Agave*, *Pittocaulon praecox (Cav.) H. Rob. & Brettell*, and *Erythrina*, all useful, on a roadside of northern Oaxaca. (**c**) *Psidium guineense Sw.*, a relative of the guayaba and important medicinal plant, in a pasture of the Sierra Norte de Oaxaca. (**d**) Roadside vegetation in the Balsas river basin, with wild *Zinnia* and other attractive species

Fig. 12.11 In southern Puebla, farmers cut and dry *Simsia lagascaeformis* DC.for winter forage of their domestic animals (Photo: Cristóbal Sánchez-Sánchez, with permission)

Other Uses of Weeds

Weeds are an important nectar and pollen source for Mexico's large—and traditional—honey production. For example, an analysis of the honey produced in Tabasco, Mexico, showed that the pollen and nectar sources were mainly weedy herbs and trees [82]. Particularly *Aldama dentata* LaLlave is a very important source species for nectar in the Yucatán peninsula.

Some weeds are used for dying, for example, species of the genera *Cuscuta*, *Bidens*, *Tagetes*, *Justicia*, *Dahlia*, *Commelina*, or *Baccharis* [83]. The Mesoamerican indigo or Mayan blue, *Indigofera suffruticosa* Mill., is also a weed.

I would like to point out that a large number of ornamental plants used throughout the tropics, and as late-summer annuals in temperate regions, originated as Mesoamerican weeds. The Asteraceae family is particularly prominent, with genera such as *Cosmos*, *Bidens*, *Sanvitalia*, *Tithonia*, *Zinnia*, *Tagetes*, *Ageratum houstonianum* Mill., and *Helianthus*. But other families, such as Amaranthaceae (*Gomphrena*), Convolvulaceae (various *Ipomoea*), Iridaceae (*Tigridia*), Lamiaceae (several *Salvia*), Solanaceae (*Browallia*), and Onagraceae (*Mirabilis)*, are also represented. Many of these are collected from weedy populations and commercialized regionally (e.g., wild species of *Tagetes* [44]). Some woody ornamentals, such as the poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch), *Brugmansia*, or *Hamelia patens* Jacq., are species of secondary vegetation.

There are also a number of miscellaneous uses, for fiber, pest control, oil and even chewing gum from the latex of *Asclepias notha* W. D. Stevens, a plant common to field margins [84].

Weeds as an Economic Component of Agricultural Production

Agricultural productivity may refer to various concepts. There is the production of useful biomass per unit area, the gross monetary value of the production per unit area, the net value to the farmer, that is gross value minus cost (which should include home consumption at replacement value but is often not taken into account), the net value to society in general, which includes the net value to the farmer, but also positive and negative externalities. Also relevant is productivity in relation to inputs (energy, water, labor, land value). Here, we look briefly at the role of useful weeds in the net production value to the farmer, and at the value for society.

Traditional agriculture is generally mixed agriculture, in space or time or both. The Mesoamerican milpa is one of the most highly developed mixed systems. However, as explained above, the mixture is composed not only of cultivated plants, but also of other species with various degrees of desirability, usefulness, and management. The cultivated plants may have subproducts as well.

Unfortunately, these secondary products are often, if not mostly, ignored when evaluating the productivity of traditional agricultural systems for two main reasons. The first reason is that they are difficult to measure or document, even by the farmers themselves. Farmers generally have a good notion of the productivity of their main crop. After all, it is their main supplier of calories or income. They are also often harvested at only one point in time during the year and are therefore more memorable. Surveys of farmers can capture this part of the productivity with relative ease.

On the other hand, documenting the secondary products is much more difficult, time-consuming, and expensive. For one, there is much more variability, as they depend to a much larger degree on the individual idiosyncrasy of the farmer and the field. Also, many of these products are harvested and used in small portions over a longer time, and frequencies and quantities are difficult to remember. There is a heavy cognitive bias (saliency bias [85]) to discount their importance, both by farmers and investigators.

The second reason is the fact that most agronomists are trained in agricultural systems with emphasis on monoculture. This is partly related to the fact that the dominant cultures today—European/Western and East Asian—depend on grains with a small stature, traditionally grown in monoculture and rotations (which is an asynchronous mixed system, but is perceived as different from synchronous mixed systems). Also, the opportunity costs of labor in prosperous societies increase motivation for simplified systems, which in turn influences the values of agronomists, policy designers, and extensionists. Thus, training and other perception biases are significant problems, particularly as they lead to perverse incentives in the design and application of agricultural policy and subsidies. Some policies with their

Table 12.2 Production of useful biomass in maize fields of the region of Nanacamilpa, Tlaxcala [86]

Biomass	t/ha
Maize grain (dry weight, as obtained from the field)	1.7
Maize stover (dry weight, as obtained from the field)	3.5
Forage plants (fresh weight)	11.5
Edible plants (fresh weight)	1.8
Medicinal plants (fresh weight)	0.2
Total useful biomass	17

The biomass was measured as used, either fresh or dry

insistence on monoculture actually lower the net value of agricultural production (see, for example, Moreno-Calles et al. [44]).

A series of local studies from central Mexico, where small farms integrating maize and animal production are common, have attempted to quantify these secondary products and multiple uses.

Almost 20 years ago, a first study in a relatively well-communicated and productive maize growing area in the highlands north of the city of Toluca showed that farmers purposefully managed maize fields to produce both quelites and forage. While quelites were relevant economically and nutritionally, forage was the main secondary product: it had an average value, after costs, that was 50 % of the value of maize grain production [20]. This showed that these secondary products were not at all trivial, economically.

I should add that a recent, still unpublished, thesis on weeds in the same village showed a drastic change: people no longer have many domestic animals, so they do not use the forage, and the use of quelites has dropped drastically. This is due to the fact that almost everybody now has other sources of income, and farming is becoming a part-time occupation.

A second study explored the absolute production of useful biomass (not the biomass actually used) in a similar but less productive area in Tlaxcala [86, 87]. Here, the value of only the maize grain would have meant a production at loss. However, as the region had a good market for maize straw (that sold at the same price per kg as maize grain), these two products together showed a small profit, after cultivation and harvest costs. However, if forage and quelites were included, the potential production was worth over 1000 US$ per ha. Table 12.2 shows the quantities of the different products obtained, the average from 30 milpas in three different villages:

These are substantial quantities for a temperate region. Of course, not all of this biomass can be used or sold. However, it constitutes a reserve and alternative if the maize crop falters. These results are comparable with those of Díaz-Betancourt et al. [88] who found 1000–3000 kg of edible plants per ha in ruderal vegetation, in both tropical and temperate regions.

A third, unpublished study by Edith Moreno, also in the highlands, documented the production of useful plants, not only in the milpa, but also on its borders (Table 12.3). As explained above, these borders are part of the production system, and harbor fruit trees, agaves, and other useful species.

Table 12.3 Case studies of individual milpas in Ixtapan del Oro, Estado de México, Mexico. Data from an unfinished thesis by Edith Moreno

Case study 1. Area: 0.25 ha.

Product	Production	Price	Cost	Net value
Maize	750 kg	\$3/kg	(see cultivation)	\$2250
Fava beans	About 50 kg	\$5/kg	1 h, \$10	\$240
Forage	A-S-O: 1200 kg	\$1.3/kg	6 h/week	\$780
Spinach greens (quelites)	12 kg in 3 months	\$10/kg	4 h	\$80
Agave for pulque	10 L/day for 4 months	\$2.5/L	1 h daily	\$1800
Fruit trees: apples	2 boxes per tree [3]: 6 boxes = 90 kg	\$8–\$5 kg	6 h	\$525

Sum: \$ 5675; cultivation cost: \$1100; net return: \$4575

Net return per ha: 18,300 pesos = 1591 US\$

Case study 2**.** Area: 0.5 ha

Product	Production	Price	Cost	Net value
Maíz	1000 kg	\$3/kg	\$1500	\$3000
Forage	J-A-S-O: 1400 kg	\$1.3/kg	4 h/week	\$1180
Spinach greens (quelites)	36 kg in 3 months	\$10/kg	5 h	\$310
Fruit trees:	1–2 boxes per tree [5] = 7 boxes (105 kg)	\$6.5/kg	8 h for all	\$1810
Apple	1 box/tree [5] = 5 boxes (75 kg)	\$12.5/kg		
Peach	6 boxes = 90 kg	\$3/kg		
Pear				

Sum: \$6300; cultivation cost: \$1500; net return: \$ 4800

Net return per ha: 9600 pesos = 865 US\$

Case study 3. Area: 0.5 ha.

Product	Production	Price	Cost	Net value
Maize	800 kg	\$3/kg		\$2400
Chilacayote (*Cucurbita ficifolia*)	15 fruit	\$10	3 h	\$120
Calabacitas (*Cucurbita pepo*); both flowers and fruit are harvested	3 bunches of flowers	\$10 (\$30)	1 h	\$70
	5 kg of fruit	\$10 (\$50)		
Forage	J-A-S-O: 1400 kg	\$1.3/kg	2 h/week	\$1500
Spinach greens (quelites)	16 kg in 3 months	\$10/kg	6 h	\$100
Ornamentals:	5 bunches	\$20 per bunch	harvest: 2 h	\$70
Flor de muerto (marigold, *Tagetes erecta*)				

Sum: \$4260; cultivation cost: 1500; net return: 2760

Net return per ha: 5520 pesos = 480 US\$

The prices are in 2006 Mexican pesos (accumulated inflation from 2006 to 2014 was 40 %); for calculations of costs, we used a value for labor of 10 Mexican pesos per hour (slightly higher than the local wage for hired field workers in 2006); the exchange rate for the dollar was approximately 11.50 pesos per dollar in the same year. The data represent actual use; they derive from a combination of interviews, observations, and measurements. *J* July, *A* August, *S* September, *O* October

The following three tables give examples of an economic analysis of individual fields with their borders to illustrate their components and relative importance of their production.

The examples illustrate clearly that maize is only a small part of a highly productive system composed of several spatial units and numerous species; various wild and weedy plants play a large role. The net values are close to the returns of intensive vegetable agriculture, and quite different from the low returns frequently cited for traditional agriculture. They depend, however, on the price of labor. Calles-Moreno et al. [44] found comparable results in the Tehuacán valley, considering the drier climate.

Apart from productivity, there are other economic considerations in which useful weeds play a role. One is the role of these plants in ameliorating risks to the food supply [44, 89, 90], both for the individual farmer and for society.

The presence of useful weeds diversifies the "portfolio" of the farmer in a way that is not possible with monocultures. If, for any reason, the main crop fails, the associated spontaneous plants assure at least some harvest [44]. In one example observed near Ixtlahuaca, Mexico, a field of onions failed due to a pest, but the owner later remarked that she earned more by selling the spontaneous *Amaranthus* and *Chenopodium* plants that appeared after the field was abandoned than she would have with the onions. It is quite common to see abandoned maize fields whose crop did not prosper, perhaps because of excessive rain or drought. Left alone, useful plants grow and are harvested, together with the abundant weeds for animal forage. The mountain Pima in Chihuahua increased their wild herb consumption drastically in a drought year with widespread crop failure [91]. Also, being able to collect spontaneous plants and sell them is an important fall-back for a large part of the population in emergencies, and for the poorest people as a regular source of income [20, 86, 92].

In another example, Martínez et al. [93] report how coffee farms, when confronted with low prices of the principal product, are not converted to other crops, but rather refocused on other intercropped species and useful spontaneous plants that are often already present. The mixed coffee garden structure is versatile and can adapt rapidly to changing markets, by simply changing efforts from attending to the coffee crop (pruning, fertilizing, etc.) to attending other species, such as fruit trees, vanilla, allspice (*Pimenta dioica* (L.) Merr.), or medicinal plants. They found over 300 useful species in the coffee gardens of the Sierra Norte de Puebla. Only one-third were cultivated, and the rest were either wild-growing or managed to some extent. Ninety species had commercial value, among them a number of weeds used for medicine, food, or ornament.

Another aspect of risk amelioration, now for society and not so much for the individual farmer, is the conservation and continuing evolution of germplasm of useful plants and relatives of crop plants. Whole societies relying on a narrow genetic base of a few inbred crop plant species is a recipe for long-term disaster. This generalized, increased risk is an externality of modern agricultural practices that has to be attended at the level of society. Ex situ conservation is often not possible or adequate [94].

In a way, small-scale, poor farmers subsidize modern agriculture in rich countries by conserving and improving crops, (weedy) crop relatives, and (weedy) potential crops, and thereby conserving genetic diversity, resistance genes of many sorts, etc., that is, function as a kind of live gene bank [95]. However, this is changing rapidly, as modernization reaches even remote areas.

This author sees only two ways to conserve the function of these systems: one is to pay knowledgeable and interested farmers sufficiently to conserve the systems, and the other is to organize commercial pathways that will sell their mixed products at a price that will recompense their now higher income expectations. Of course, appropriate comparative research on the actual costs and benefits, both for farmers and for society, of modern (simplified) and traditional (diverse) systems may also improve appreciation of traditional systems and the direction of public policy.

A third aspect of risk amelioration is the importance of agricultural diversity, including weeds and the knowledge and experience associated with traditional, low-external-input agroecosystems, in maintaining alternatives to current systems. Modern agriculture is extremely dependent on external energy inputs; agricultural products are often energy negative when they reach the dinner plate of a modern urban dweller [96, 97]. Traditional agroecosystems, by necessity, are always highly energy efficient [96]. The distribution of energy (and its subproducts, such as agrochemicals and improved seeds), in turn, depends on a network of communications of many types, all of which are vulnerable to sudden disruptions, from both natural and man-made causes. And, of course, there is no guarantee that external energy prices will remain low enough to continue making energy-negative food viable. The maintenance of alternatives in cases of catastrophes or drastic changes of circumstances is a quintessential public good, which must be assumed by society as a whole. It requires dedicated strategies. Both germplasm and local knowledge are impossible or extremely difficult and expensive to resurrect, once they have disappeared. As they are part of a larger system, they can be maintained ex situ in only a very limited way.

Perspectives

Weeds are an important and relevant part of Mesoamerican agricultural productivity. They also have a number of general ecological and economic effects that should be explored more thoroughly.

The ethnobotany of Mexican weeds has been studied unevenly. The focus has been on useful plants and a few regions, while other people-plants interactions have been overlooked to some extent.

Agrestal edible weeds used as quelites are relatively well known, at least those of the highlands and the humid mountain areas where their use is most obvious (Fig. 12.12). There is less information from the arid north and the humid and dry tropics. Some data on quantities and qualities of these foods exist, but not nearly enough to be able to make well-supported generalizations.

Fig. 12.12 The section of edible herbs in the large wholesale market (Central de Abasto) of Mexico City

Some attention has been paid to agrestal weeds as forage, medicinal, nectar source, dye plants or for handicrafts, but generally only by a single investigator or group and always very locally. It is not yet possible to give a national overview.

In general, this contribution argues for viewing agrestal and ruderal weeds separately. Even though there is a good amount of species overlap, the ecology and selection pressures are distinct. This appears to apply especially to medicinal plants; several well-documented examples show that ruderal vegetation is the principal source of medicinal plants, either in first or second place, after species cultivated in home gardens; agrestal weeds are a minor source. However, the examples from the dry and humid lowland tropics are still few. Ruderal vegetation has been neglected scientifically but is relevant from many points of view—among them, landscape management, ethnopharmacognosy, conservation and invasive plant science. Invasive plants in Mexico, particularly the introduced African forage grasses, tend to occupy ruderal habitats first and are often very dominant and intolerant. They frequently displace the native vegetation of these sites, which exotic agrestal weeds rarely do.

Another area that has received at least some quantitative attention is in situ selection for favorable traits, particularly in edible, agrestal weeds. Medicinal plants or nectar sources should be included in these investigations.

Two areas that have important practical applications are much under-researched. While ethnobotanists commonly speak of the highly adapted milpa system and enumerate its parts, there is very little quantitative analysis of the ecological and economic components, productivity in relationship with other factors, the role of "secondary" products such as useful weeds, sustainability, risk, or the decision processes of the farmers, all of which are good ethnobotanical subjects. Positive examples that integrate various aspects of the milpa agriculture, though also with emphasis on cultivated plants, are summaries of studies on milpas in Yucatán and Chiapas published as books [18, 98–100]. Preliminary and very local data show that the milpa is highly productive, if all in- and outputs are considered. It is astounding that a subject such as this—highly important for understanding and guiding agricultural development—has not received more attention.

Another area that has been explored only very little is the ecology and the adaptations of Mesoamerican weeds. This contribution shows with a few examples that generalizations on Old World weeds do not always apply to New World synanthropic plants, as the selection pressures are distinct. However, even basic data, such as the pollination type, is not known for most native weeds. I suggest this to be a highly interesting subject area for collaborative investigations between ethnobotanists and evolutionary ecologists.

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Chapter 13
Phylogeographical Approaches to the Study of Plant Domestication, with Special Emphasis on Perennial Plants

Xitlali Aguirre-Dugua and Antonio González-Rodríguez

Abstract This chapter analyzes the use of phylogeography for the study of plant domestication as an evolutionary process. First, a synthesis of phylogeography is presented, together with an outline of its main tools, scope, and limitations regarding the study of the origin and evolution of domesticated species. Later, these issues are analyzed in the case of domesticated perennial species, mainly trees. For appraising the value of nuclear and organelle DNA data on the study of domestication processes, we review phylogeographical and genetic studies on ten selected domesticated perennial species from the Old and New World, propagated through cuttings or seeds. Bottlenecks and introgression occurrence, identification of geographical origins, and identity of wild parents are particularly discussed. Finally, the phylogeographical patterns of these species are analyzed in the light of plant domestication theory, making special emphasis on the role of ethnobotanical studies for interpreting genetic data and building new hypothesis and models.

Keywords Tree domestication • Artificial selection • Human dispersion • Population differentiation • Gene flow

Introduction

Domestication is an evolutionary process in which humans fix in a population, by means of artificial selection, the desired hereditary variants that satisfy their needs (food, utilitarian, and aesthetics) and that distinguish the domesticated taxon from

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its wild progenitor [1, 2]. Human groups started to cultivate and domesticate plants independently in different parts of the world around 12,000 years ago, driven mainly by the scarcity of wild resources caused by the climatic changes that mark the division between the Pleistocene and Holocene [3]. Based on archaeological evidence, it is recognized that human societies gradually changed from a nomad hunter-gatherer lifestyle to a more sedentary and structured village society, shifting from the collection of wild plants, to their pre-domestication cultivation and then to their domestication through agriculture, horticulture, and forestry strategies in anthropogenic environments [3, 4].

The first systematic studies on the origin of domesticated plants were developed by the French naturalist Alphonse de Candolle [5], the Russian geneticist Nikolai I. Vavilov (who identified eight “centers of development of forms” in the world as valuable sources of germplasm for agriculture, now commonly known as centers of diversity) [6], and North American agronomist Jack R. Harlan [7] who gave more detail to these centers and integrated information on the origin of agriculture and animal husbandry (Table 13.1). Biological sciences then began working next to agronomists and archaeologists on the search for the origin of domesticated species, first with morphoanatomical studies, cytogenetic experiments and controlled breeding programs, and more recently with the help of molecular biology [3, 8, 9]. Since the 1980s, the development of molecular techniques based on allozymes and fragments/sequences of DNA of nuclear (nDNA), chloroplast (cpDNA) and mitochondrial (mtDNA) origin opened new avenues of research that have broadened our understanding of the origins of domesticated species. These tools have also contributed to the development of a more comprehensive theory of biological evolution, given that domesticated taxa represent useful model systems for the analysis of genetic, morphological, physiological, and behavioral changes of living beings, just as Darwin envisioned it 150 years ago [10, 11].

From an evolutionary perspective, domestication is conceived, in an analogous manner to speciation, as a temporal and spatial process of population differentiation guided by artificial selection that generates new lineages. The speed of this differentiation process depends on the strength of artificial selection, gene flow between selected and wild individuals, effective population size, and the organism’s life span [12].

Integrating both genealogy and geography, the field of phylogeography is a useful framework for the analysis of the domestication processes since it represents the crossroad between population genetics, which addresses microevolutionary forces at the individual and population level, and phylogenetics, related to the differentiation of new lineages or evolutionary units [13]. In this chapter we will present a brief overview of the discipline of phylogeography, its scope and primary tools, and will discuss them in terms of their main use, reach, and limits in the research for the origin and evolution of domesticated species. Because of the success and growth of this field in the last decade, it is not our purpose to cover all aspects of phylogeography; we hope the reader will find a more detailed treatment of each topic in the references included herein. In the second part of the chapter, we will analyze these issues in the special case of domesticated long-lived perennial plants, mainly trees.

Table 13.1 Different approaches to the study of the origins of domesticated plants

Field	Main interest	Tools	Analysis units	Perspective
Agronomy and anthropology (Vavilov and Harlan)	Identify areas with promising varieties for breeding programs. Locate regions where agriculture first appeared	Taxonomy	Races	Biogeographic
		Morfometry	Cultivars	
		History/archaeology	Species (morphological and biological concepts)	
		Cytogenetics		
Population genetics	Conservation	Genetic statistics	Individuals	Microevolutionary
	Understand species’ natural history and ecology		Populations	
Phylogenetics	Conservation	Phylogenetic tree reconstruction	Lineages	Macroevolutionary
	Identify wild parents		Species (evolutionary concept)	
	Determine successive events of differentiation/diffusion			
Phylogeography	Characterize genealogical history of intraspecific lineages in time and space	Haplotype networks	Populations	Micro–macro evolutionary
		Phylogenetic tree reconstruction	Species (cohesive concept)	Biogeographic
		Coalescent theory		
	Conservation	Geographic Information Systems		
	Identify dispersion and hybridization events			

This group of plants outstands for its high phylogenetic diversity and for its ecological characteristics that include sexual and asexual reproduction, exogamous reproductive systems, and high levels of gene flow among populations. By reviewing the literature on ten selected domesticated perennial species, we aim at analyzing how genetic and phylogeographic data from nuclear and organelle DNA has enriched our knowledge on their particular histories, including the intensity of the genetic bottlenecks they have encountered, their geographical origin and the identity of their wild progenitors, as well as the occurrence of introgression events. We will then discuss these phylogeographic patterns in the light of the theory on perennial plant domestication and will consider the role of ethnobotany for enriching genetic and phylogeographic studies in issues such as documenting artificial selection practices and human-mediated gene flow processes.

Phylogeography: An Integrative Field

Phylogeography is the discipline that analyzes the spatial arrangement of genetic lineages within and among closely related species. By focusing on gene trees of neutral loci from individuals in populations, phylogeographical analyses aim to understand the historical and contemporaneous forces that have produced the current genealogical architecture of populations and species [14, 15]. As gene trees carry the signature of a species' demographic past, it is intended that their analysis in a geographical context can reveal the relationships between population phenomena (e.g., migration, population growth/bottlenecks, selection, and gene drift), species distribution, and the mechanisms driving speciation [14]. However, although phylogeography uses the historical information contained in gene trees, it is not a simple extension of phylogenetics to the intraspecific level; it rather characterizes population subdivision in order to identify historical geographic patterns of genealogical structure throughout the distribution of a species and to distinguish them from those caused by modern gene flow [14, 16, 17]. By integrating population genetics and phylogenetics in a geographical framework, phylogeographic analyses are useful for addressing domestication processes because domesticated species commonly include many evolutionary lineages with different degrees of divergence, produced by diverse population differentiation processes in a brief and geologically recent time window.

Molecular Tools of Phylogeography

Molecular markers are the main source of information in phylogeography. Because the straightforward reconstruction of gene genealogies is a fundamental step in all phylogeographic studies, cytoplasmic DNA was originally proposed to be the marker of choice for this purpose. Particularly, mitochondrial DNA (mtDNA) was thought to be ideal for phylogeographic studies in animals because of its ubiquity, ease of isolation, simple structure lacking repetitive DNA, transposable elements, pseudogenes and introns, simple and usually uniparental inheritance without recombination, and considerable degree of intraspecific polymorphism due to a high mutation rate [15, 18].

In contrast to their early success in animals, phylogeographic studies in plants were slower to develop. One of the main reasons was the problem of detecting appropriate levels of genetic variation in plant genomes. The plant mtDNA is characterized by low rates of nucleotide substitution and is prone to extensive recombination, making it inadequate for generating intraspecific gene genealogies [16, 19]. Chloroplast DNA (cpDNA) is a larger and more complex molecule than mtDNA (about 120–170 kilobases in comparison to the 16–20 kilobases of mtDNA) and more effort was required for its characterization and the identification of useful regions for phylogeographic studies. The mutation rate is variable at different regions of cpDNA, with most variation occurring in the single-copy regions, particularly in spacing sequences that separate coding genes [16, 20]. Simple sequence repeats (SSR) or microsatellites have also been identified in plant cpDNA and these loci usually display not only significant variation but also frequent homoplasy [20].

More recently, an emphasis has been put in employing multilocus data for phylogeographic reconstruction, particularly with the advent of coalescent theory and statistical phylogeography (see below). In this respect, mtDNA or cpDNA data are limited because these nonrecombining, uniparentally transmitted genomes are inherited as a unit and therefore represent a single locus in practice [21] (Fig. 13.1). One of the important realizations derived from coalescent theory is that gene trees are expected to vary among different loci, not only for stochastic but also for other

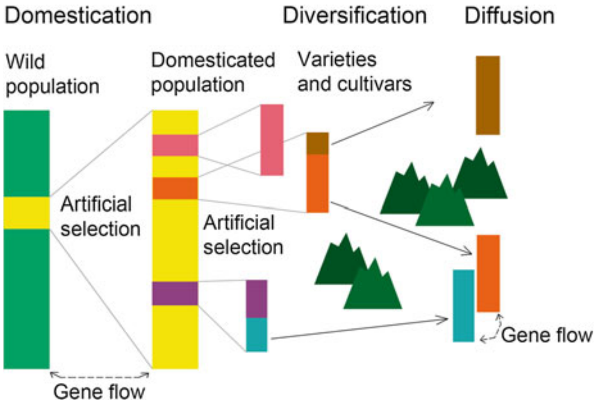

Fig. 13.1 Classical perspective on domestication as the foundation of a new population based on a subsample of wild individuals. Subsequently, artificial selection and drift drive the differentiation process among wild and domesticated populations. Diversification of the domesticated pool can be driven by disruptive selection forces, diffusion to new regions with contrasting environmental conditions, and hybridization with wild parents and/or other domesticated varieties. It is traditionally assumed that domestication and geographical diffusion events lead to genetic bottlenecks

reasons [22]. Consequently, basing phylogeographic inference on the patterns exhibited by a single locus can be misleading. Nuclear DNA (nDNA) offers not only a potentially inexhaustible source of informative genetic variation but also considerable challenges in its application to phylogeographic studies. First, regions with appropriate levels of variation must be identified since mutation rates in the nDNA are usually low. Secondly, single-copy regions are preferable over regions with multiple copies because for the latter, the possibility of presence of pseudogenes or paralogous variants is higher [21, 23]. Thirdly, recombination has to be taken into account, but fortunately several algorithms are currently available for this purpose [24].

The current molecular toolbox for phylogeographic studies includes several techniques for detecting and analyzing variation at mtDNA, cpDNA, and nDNA. Variation at the cpDNA of plants has become quite accessible through the development of universal primer pairs for the amplification through the polymerase chain reaction (PCR) of highly variable loci as intergenic spacers and introns [25, 26]. The amplified regions then can be sequenced, which is the most informative approach, or analyzed with restriction enzymes to produce restriction fragment length polymorphisms (PCR-RFLP). Primer pairs for the amplification of cpDNA SSRs have also been developed, differing in their degree of conservation and utility among groups of plants [27]. A common current practice is to mark one of the primers (usually the forward primer) with a fluorescent label that can be detected in an automatic capillary sequencer. Amplified fragments are separated electrophoretically and scored as different alleles depending on their size (in base pairs). Basically, these same techniques (sequencing, PCR-RFLP, size analysis of SSR alleles) can be applied for the analysis of nDNA, except that universal or consensus regions are scarce even for relatively small taxonomic groups.

A useful and relatively simple molecular technique that allows the multilocus analysis of nDNA is known as Amplified Fragment Length Polymorphism (AFLP). This technique is based on the digestion of genomic DNA with two different restriction enzymes, followed by the ligation of adaptors to the sticky ends of the restriction fragments. In this way, thousands of adapted fragments are generated, but only a subset of these is selected for amplification through PCR. The selection is achieved using primers that are complementary to the sequence of the adaptor but that also have between one and three arbitrary base pairs that extend into the unknown portion of the fragment, and therefore can be complementary or not depending on chance. In this way, the number of amplified fragments is reduced by factors of 4, 16, or 64 if an extension of one, two, or three base pairs is used. Since many combinations of restriction enzymes and primers can be used, the number of resulting fragments is virtually unlimited. In practice, a few hundred fragments are ideal, obtained by using two or three primer/enzyme combinations. The scoring of the fragments can be performed through polyacrylamide gel electrophoresis or capillary electrophoresis in an automatic sequencer, which make it possible to resolve fragments that differ in size by a single base pair [28].

The advantages of the AFLP technique are that it can be readily applied to any organism and no initial investment in primer development or sequence analysis is required. It is a relatively cheap, easy, fast, and reliable method to generate hundreds of informative genetic markers. However, a main disadvantage is the difficulty of assessing the homology among markers of the same molecular size; they also are dominant markers, i.e., a state of "fragment present" can equally correspond to an individual that is homozygous or heterozygous for the "presence" allele [28, 29].

The development of next-generation sequencing techniques and the increasing advances in genomics are making it feasible to access much larger amounts of data for many different evolutionary studies, including phylogeography. It is now possible to analyze single nucleotide polymorphisms (SNPs) scattered across the whole genome of the organism of interest. SNPs are abundant, codominant, evolve in a manner well described by simple mutation models, and represent a suite of unlinked nuclear genetic loci that can capture a genome-wide picture of population history [30]. Given that SNPs have a lower mutation rate than other genetic markers (e.g., microsatellites), homoplasy is usually not a problem. On the other hand, SNPs have a maximum of only four character states (A, T, G, C) making them less informative than microsatellites, but this limitation can be compensated by the much higher number of SNP loci usually available. It has been suggested that SNPs will become the marker of choice for multilocus phylogeographic analyses [31, 32].

Descriptive Analytical Approaches in Phylogeography

When trying to reconstruct the history of domesticated species, the first step toward phylogeographic inference is based on the identification of genetic relationships among the groups sampled, which includes the domesticated lineage (one population or many, representing different varieties, for example) and wild populations (among which, hopefully, the direct descendants of the wild ancestral population that gave rise to the domesticated population are represented). For this purpose, a wide array of methods is available. Most commonly used with anonymous nuclear markers such as AFLPs or ISSRs, dendrograms or distance grouping analysis (such as the Unweighted Pair Group Method with Arithmetic Mean—UPGMA and Neighbor Joining—NJ), and multivariate methods (hierarchical clustering and principal coordinate analysis—PCoA) rely on measures of genetic distance among populations, which are directly affected by the loss of alleles associated to the domestication genetic bottleneck. Assignment methods (e.g., *Structure* [33]) based on multilocus nuclear markers such as SSRs, AFLPs, or SNPs have also been applied in order to identify the most probable number of genetically distinct groups (populations) and assign individuals to such groups in a probabilistic manner, something that allows for the identification of hybrid individuals (i.e., admixed genotypes).

A more historical perspective is achieved through the construction of phylogenetic trees and haplotype networks. Phylogenetic trees are commonly used with sequence data (single and multilocus) and employ evolutionary models that place different weights on each kind of substitution, i.e., they are based on character states. However, in this case, trees are constructed with the aim of understanding relationships among haplotypes and not among certain taxa, as in traditional phylogenetics. The result is the grouping of haplotypes in clades that display a bifurcating pattern (although sometimes the branching order cannot be defined and a politomy remains). Phylogenetic reconstruction can be achieved through a wide array of methods (e.g., parsimony, maximum likelihood, Bayesian statistics) and can use statistical tools (e.g., bootstrap, posterior Bayesian probabilities) for evaluating branch's support, which represents the strength of the genealogical signal in the sample that defines the relationships among groups. Additionally, phylogenetic trees can be rooted with an outgroup to polarize the tree, i.e., to define ascent–descent relationships among the oldest node representing the last common ancestor of the samples including the outgroup, and the remaining younger nodes closest to the tips of the tree [34]. Molecular clocks based on estimated substitution rates and calibration points can be used for the estimation of the age of the nodes, i.e., for the timing of divergence events [35].

However, when applying methods of phylogenetic reconstruction to intraspecific data, it should be taken into account that evolutionary relationships above and below the species level are qualitatively different. Within a species, relationships among alleles at a given locus are the result of a comparatively small number of recent mutations, recombination, and sexual reproduction. Hennig [36] referred to this type of relationships as tokogenetic, to differentiate them from the strictly hierarchical, deeper divergences that characterize phylogenetic relationships among alleles found in different species, which are the product of reproductive isolation, independent mutation, and lineage sorting over a longer period of time, leading to separate gene pools.

As an alternative to phylogenetic trees, haplotype networks can better account for processes acting at the species level, and adequately represent the presence of persistent ancestral haplotypes, multifurcations, reticulations, and homoplasy [24]. Unlike phylogenetic trees, connections among nodes in a network can show cycles, representing a pattern that is not strictly bifurcating. Currently, there are several methods to construct haplotype networks from sequence or SSR data, such as median-joining and statistical parsimony [24, 37]. Haplotype networks built from SSR data commonly assume that microsatellite length is increased or decreased by one repeat unit at a time (stepwise mutation model, SMM [38]). A two-phase model (TPM) can also be used, where mutations can change the repeat length by one unit (with probability p) or by more than one unit (with probability $1-p$, multiunit mutations being geometrically distributed [39]). When sequence data are used for defining haplotypes, it is possible to consider different evolutionary models, just as in phylogenetic tree reconstruction.

Coalescent theory provides several explicit predictions that are directly relevant to the interpretation of haplotype networks. Older haplotypes are expected to have a greater frequency, to be more widespread geographically and to be situated in the interior of the network (that is, to have more than one connection with younger, derived haplotypes). In contrast, low-frequency haplotypes are more likely to be connected to more common haplotypes than to other low frequency haplotypes. Also, rare haplotypes are more likely to be derived from other haplotypes in the same population than from haplotypes in other populations. According to this, the root of the network (i.e., the oldest ancestral haplotype) is considered to be the most frequent haplotype, although the number of connections and the position of a given haplotype can also be used to assign root probabilities [24, 40].

Once they have reconstructed the genealogical relationships between populations through these methods, many phylogeographic studies follow a descriptive approach for interpreting them. Descriptive studies commonly depict the genetic patterns observed in the sample (number of haplotypes, their frequency and geographical distribution, the detected amounts of genetic diversity, and its structuring according to different summary statistics), superimpose the reconstructed genealogy over the geography, and interpret their data directly in order to infer the history of the sampled populations. This strategy was commonly used by those studies published in the first decade after the seminar publication by Avise et al. [18], and is still applied today by many researchers. However, it has been described (and criticized) as a *post hoc* narrative and other methods have since then been proposed as more reliable (see next sections).

Nested Clade Phylogeographic Analysis

In order to go beyond the simple description of the geographical distribution of genetic variants from different populations, Templeton et al. [41] proposed the Nested Clade Phylogeographic Analysis (NCPA), a guideline for interpreting the agreement between the geographical distribution of haplotypes and their genealogical relationships, according to particular historical scenarios. In general terms, this method applies to a step-wise inference key based on the relative position of single-locus haplotypes in an haplotype network and their grouping in hierarchically nested clades, together with the geographical distance that separates such haplotypes. For example, according to NCPA, in a basic pattern of long-term restricted gene flow, it is expected that the oldest haplotypes, located at the center of the haplotype network, should be widely distributed while the more recent mutations should be located at the tips of the network and remain localized in the areas where they originate [42]. By looking at different patterns of the geographical spread of more or less related haplotypes, the NCPA inference key can reveal other scenarios such as restricted gene flow with isolation by distance, range expansions, long-distance dispersal events (i.e., colonization), and allopatric fragmentation. Significance of the inferred scenario is evaluated through a permutation test of the haplotypes within the nested clades (i.e., a test for the null hypothesis of no correlation between geography and genealogy) [42]. The method was later modified and extended to include multi-locus cross-validation and the testing of specific phylogeographical hypotheses through a likelihood ratio testing framework [43–47]. These modifications were a response to criticisms by different authors who found the method ambiguous and lacking statistical rigor given that the inference key and permutation test showed to be prone to a high false-positive rate [48–51]. A strong debate then followed between those defending the method and those criticizing it, who rather put forward model-based approaches [52–61]. In the last 5 years, there has been a sharp decline in the use of NCPA as the central method of phylogeographic studies, but it is still applied in conjunction with phylogenetics, population genetics, and coalescent-based methods in order to propose and analyze plausible hypotheses on the demography and biogeography of populations according to species biology and landscape history [52, 62–64]. New procedures that incorporate Approximate Bayesian Computation (ABC) to the construction of haplotype networks and clustering seem to be the next stage for NCPA (see [65]).

Coalescent Theory and Statistical Phylogeography

It has been recognized that direct interpretation of demographic and biogeographic processes from the genealogical patterns showed by a group of populations can lead to an overinterpretation of data, as they are subjected to the stochasticity of demographic processes: different histories can lead to a similar genealogical structure and one history can produce diverse genealogical structures. With this in mind, coalescent-based approaches have been developed in the emerging field of statistical phylogeography to test explicit hypotheses that underlie observed phylogeographic patterns.

This approach is based on the reconstruction, from the present to the past, of the historical relationships between the alleles from a sample by making them converge or coalesce in their ancestral alleles [66]. The analysis of the depth and ramification structure of coalescence trees derived from empirical data is used to reveal the demographic history of the populations through the estimation of parameters such as effective population size (coalescence points tend to be older when effective population size is high because the probability of lineage extinction is smaller), amount of gene flow (if present, some alleles of one population will coalesce in a different population), and the action of genetic drift or selection (some branches of the tree disappear while others proliferate) [14]. Statistical methods that simulate coalescent processes have therefore been developed to test a priori defined models (i.e., phylogeographic histories), which means that none of the models is “true” and that the reconstructed genealogy is not directly interpreted but considered as a variable that links the observed data to every proposed model [17].

Coalescent-based methods can model a wide array of possible genealogies according to previously defined parameters that depend on the proposed hypothesis, and they evaluate the probability of the observed genealogy with Bayesian or maximum likelihood approximations. Alternatively, if there are no previously defined hypotheses, they can estimate the most probable demographic parameters that can account for the observed data and provide confidence intervals. Such parameters can include mutation rate, effective population size, rate of population growth, population subdivision, gene flow, divergence times, and selection [67]. On the basis of these theoretical advances, several algorithms have been developed that can be applied to empirical data to obtain estimates of the historical demographic dynamics of populations. For example, the Isolation-with-Migration model (IM) considers an ancestral population diverging into two derived populations that continue to exchange migrants during the divergence process [68, 69], a scenario that fits very well a domestication event. This model includes six demographic parameters (divergence time, migration from population one to two, migration from population two to one, effective population size of the two derived populations, and effective population size of the ancestral population). These six parameters can be estimated from adequate empirical molecular data with the IMa program, which is an implementation of the IM model [70].

Another method that has become popular to infer population demographic history is the Bayesian Skyline Plot [71]. This algorithm, implemented in the BEAST (Bayesian Evolutionary Analysis Sampling Trees), allows the estimation of historical patterns of population size from a gene genealogy without the need for a priori restrictions on possible demographic models [72].

However, Knowles [73] points out that phylogeographic hypothesis testing can be sensitive to the kind and number of parameters included: models that represent many processes at a time can be biologically more realistic but also more complex and, in consequence, be overthrown by the amount of data necessary to distinguish between alternative hypotheses and a greater computational capacity. As well, Templeton [58, 59] has criticized model-based approaches by considering that they evaluate a finite set of arbitrary chosen phylogeographic alternatives, that they are influenced by subjective assumptions on the parameters being estimated, and that their statistical results are hardly interpretable.

Nevertheless, the definition of hypothetical models can be based on independent sources about past events such as the location of populations, times of their probable isolation/divergence, or events such as climatic changes or barrier appearance [17]. While information sources for wild species can be fossils and palaeoclimatic data, in domesticated species, it is possible to include parameters based on reproductive biology studies, as well as archaeological, anthropological, and documentary evidences [74]. For example, experiments between the domesticated taxon and their wild parents can provide estimates of gene flow, and archaeobotanical samples dated with 14C or AMS [75–77] can suggest divergence times or, at least, a superior limit for the divergence event (i.e., when the domesticated morphology is already observed). Macro and microbotanical evidences can also suggest diffusion routes to new areas and, in consequence, differentiation processes through bottlenecks or ecological adaptation of cultivars [78].

The Paradigm of the Domestication Bottleneck

The classic perspective of the domestication process considers that the domesticated population harbors a reduced fraction of the total genetic variation present in its wild progenitor because only a subsample of the available diversity of the wild species is selected by man [79, 80]. The result of this sampling process is a genetic bottleneck at the population level and the differentiation of a new (domesticated) lineage from the wild ancestral lineage at a genealogical level. From this moment on, with the gradual appearance of barriers to gene flow (elimination of wild-type individuals in the domesticated stock, negative natural selection of domestication traits in wild populations, selection for differential phenology, geographical isolation), both populations/lineages start to accumulate independent mutations and continue evolving in their respective environments. Following the same line of reasoning, posterior diffusion events to other geographical areas based on subsamples of the domesticated population will also lead to genetic bottlenecks [81]; geographical isolation and adaptation to new environmental conditions can be additional factors that lead to population differentiation.

With this in mind, it has been traditionally assumed that when the domesticated taxon has been originated by one domestication event, all populations will form a monophyletic clade (or, in the case of haplotype networks, will belong to the same haplotype group). Additional lines of evidence that suggest a single origin are the presence of a single neutral genetic variant in different cultivars of the domesticated pool while the wild taxon presents many variants (especially if this uniformity is displayed by several loci) and the identification of a single gene or group of genes responsible for a given domestication trait in different cultivars [82, 83]. If, in contrast, the domesticated taxon is the product of multiple domestication events, i.e., of the selection of a different subsample from more than one wild progenitor in different places, a polyphyletic pattern will emerge. Multiple origins can also be suspected if a given domestication trait is governed by different mutations in different cultivars and if the domesticated pool presents many neutral variants equally found in different or geographically separated wild populations [2, 82, 83]. As a corollary, the identification of the closest wild relative rests upon the sharing of particular haplotypes between the domesticated taxon and a given wild population or the topology of the reconstructed phylogenetic tree. If domestication occurs in sympatry with the wild progenitor, then the area where the domestication event took place (i.e., the center of origin) can be identified as the area where the closest wild relative is found. However, equaling the present distribution of the closest wild parent to the area of domestication can be misleading if its current distribution is not the same it had when the domestication took place, or if there are undiscovered or extinct populations that could be closest to the domesticated taxon [74].

Additionally, it has been proposed that those branches that diverge early from their common wild progenitor would be representative of the first stages of domestication, while the more derived domesticated varieties would be those of more recent differentiation and whose geographic areas probably represent where the domesticated germplasm has been recently introduced [84]. However, it is important to notice that the identification of cultivars as "primitive" or "basal" because they branch early (near the base of the tree) can be misleading. An early branching lineage is, in fact, a lineage with a small number of representatives (either because it has not diversified, it has had a high extinction rate, or it was poorly sampled in the study) whose age is the same, not older, as its richer sister clade [85, 86]. At the same time, inferring biogeographic scenarios of dispersal and proposing ancestral areas where the initial steps toward domestication took place based on the geographical location of a lineage misinterpreted as "basal" is therefore not possible based on tree topology and the distribution of terminal taxa alone [86]. Nevertheless, independent information from biogeographical, archaeological, and historical sources such as the distribution of the putative wild progenitor and the presence of certain cultivars in a given area at a certain period of time can allow for the inferring of the most probable dispersal scenario among those possible for a given tree topology.

Why Genetic Patterns Are Not That Easy to Interpret: Some Problems When Facing Data

The main issue regarding data interpretation in every phylogeographic or phylogenetic analysis is the incongruence that can exist between gene trees and population/species trees [87]. Phylogeographic patterns can be obscured when the bottleneck has not been severe and the effective population size of the domesticated population remains relatively large. In that case, it can be difficult to discern if two genetically close populations are similar because of the presence or gene flow or by the retention of ancestral polymorphisms [88]. The stochastic nature of neutral gene inheritance, together with stochastic demographic histories, produces trees that are not representative of the history of the species. This phenomenon harbors particular relevance when working with recently diverged populations or species such as domesticated ones. This is why it is highly recommended to use multiple loci in order to increase the probability of recovering the true species tree [14, 21]. As previously mentioned, methods based on the coalescent are intended to deal with such genealogical stochasticity through a probabilistic approach.

Besides these concerns, there exist additional issues specifically related to the study of domesticated species history. Two of them are related to the amount and nature of the data that can be obtained: the absence of a phylogeographic structure in the analyzed populations, and the sampling of only extant populations, both domesticated and wild. As previously discussed, the identification of the wild progenitor and the pinpointing of the probable center of origin rests on the identification of shared haplotypes between the domesticated populations and a given wild parent or, when using a phylogenetic approach, by the identification of the closest wild parent. However, when phylogeographic signals in the wild pool are weak, this cannot be achieved with confidence; humans have severely perturbed wild environments since the beginning of the Holocene and have equally been responsible for the movement of domesticated individuals, blurring historical phylogeographic patterns [89]. Phylogeographic signal can also be lost if hybridization between the domesticated taxon and its wild progenitor occurs, obscuring the original founder effect patterns by mixing their genomes [82]. High levels of gene flow can also obscure the expected phylogeographic patterns of multiple domestication events because domesticated populations will look more similar to each other than to their respective wild progenitors due to gene exchange [90]. When this happens, the most common approach is Vavilov's method: areas with the greater genetic diversity are the more likely centers of origin (for example *Solanum melongena* [91]). Secondly, a general problem faced by any analysis based on genetic data and that affects the interpretation of patterns about the geography and time of domestication is that sampling is based on present-day representatives of wild populations, landraces, and modern cultivars. For example, when many wild progenitors have contributed in the past to the extant domesticate but most of them have not persisted because of extirpations and range variation caused by climatic and environmental changes, both by natural and human causes [92], the present-day domesticate will appear associated to only one relative, the closest it has among those lineages that survived. This phenomenon most probably accounts for many of the discrepancies observed between genetic data and those processes inferred by the archaeological record [83]. However, the inclusion of samples from herbarium specimens [93] and the analysis of ancient DNA obtained from archaeobotanical remains [94] offers the possibility of minimizing this problem.

On the other hand, different authors have signaled some of the shortcomings of phylogenetic tools and their underlying assumptions when applied to the reconstruction of domestication history, mainly regarding the estimation of divergence times as well as the interpretation of tree topology. It has been signaled that there are problems associated with the timescale of dendrograms when wild relatives are included in the phylogenetic analyses because they diverged much more time before than the domesticate in relation to its wild progenitor (see [95]). It has also been pointed out that, together with limitations regarding the estimation of divergence times in general (such as the usage of fossil-based calibration points [35]), molecular clocks obtained from evolutionary processes observed at the phylogenetic scale cannot be applied to population divergence processes that are occurring at an intraspecific scale. Apparently, the molecular clock "ticks" more rapidly as the timescale decreases, that is, that instead of being constant over time, substitution rate is accelerated when dealing with genetic data whose mutations are more recent [96]. This time-dependency of molecular rates is most likely associated to a near-neutral model of evolution where slightly deleterious new mutations are removed from the population by purifying selection so that they do not persist over long evolutionary time frames, although they are detected when analyzing population-level data. Saturation at mutational hotspots could also account for an apparent decrease in mutation rate at deeper times. As a whole, this would mean that recent polymorphisms contribute to an apparent increase in molecular rates toward the present (especially for the last 1–2 My [96]). The main consequence of this phenomenon is that if a molecular clock based on evolutionary rates derived from species whose most recent common ancestor existed millions of years ago is applied to a dataset of recently diverged populations, the timing of the domestication event will be pushed deep into the past; in other words, the recently diverged populations will present a high degree of variation because slightly deleterious mutations would have not been yet purged and the slow molecular clock will overestimate the time it would take to produce such variation [89]. By pre-dating phenomena that have happened during the Holocene, it is not surprising that estimates based on molecular clocks differ from those based on archaeological findings [96].

The discrepancy between genetic and archaeological data has also led to the questioning of the assumptions on the tempo and mode of domestication that underlie the apparently straightforward interpretation of genetic patterns shown by the topology of phylogenetic trees. As described earlier, it is common to infer the number of domestication events that gave rise to a crop according to the topology of a phylogenetic tree (a single domestication event within a single geographic locality will lead to monophyly while two or more events in different areas will produce a polyphyletic pattern because each domestication event would be genetically independent [82]). However, it could also be the case that, instead of being the result of a bottleneck, the crop was a composite product of different selection events taking place at different geographical localities. In the presence of a weaker artificial selection process and a predomestication period more lengthy and geographically extended, there would be enough time for recurrent gene flow among domesticated populations and wild relatives to lower the likelihood that the crop would be associated with a narrow geographical range and that multiple domestications would be genetically independent (the so-called protracted model of domestication [97]). Under this scenario, crops with multiple origins would appear monophyletic because of gene flow (according to computer simulations, populations monophyly would be attained in ~2N generations, i.e., on a time that depends on the size of the domesticated population [97]), in which case monophyly would be of little help for differentiating between multiple and single domestication events [98]. Nevertheless, in a critical reconsideration of the proposal of Allaby et al. [97], Ross-Ibarra and Gaut [99] found that single domestication events are more likely to show a monophyletic pattern, even with larger effective population sizes, and that although two domesticated pools with admixture can indeed attain monophyly, this happens much longer (one order of magnitude, ~40N generations) after their initial domestication. Additionally, it would be necessary to take into account the reproductive biology of the plants under domestication, as the amount of gene flow necessary to lose the genetic independence among localities would depend on the species' outcrossing rate [100], although the proponents of the protracted model signal that monophyly is attained even in the case of self-pollinating species [98].

In a similar way, tree-based methods (e.g., parsimony, Neighbor-Joining, UPGMA) have been signaled as inappropriate for the reconstruction of the historical relationships below the species level. They have been criticized for assuming a strong hierarchical, bifurcating structure in the data where different branches evolve independently from one another, while historical relationships below the species level commonly include reticulate processes because of gene flow, which leads to the sharing of neutral loci between populations (reticulate processes include recombination as well, but as previously mentioned one should not use recombinant loci in phylogeographic analyses). Tree-based methods, as it is their purpose, will attempt to find the tree-like structure that best explains the observed patterns in the data even in the presence of reticulation [101] and, as a result, the appearance of a monophyletic group cannot be considered as a reliable indicator of the taxon being a distinct evolutionary lineage. Fortunately, low bootstrap support for some branches can correctly suggest the presence of introgression [102]. Network methods that allow for cycles (or loops) that represent non-dichotomous relationships between individuals have therefore been signaled as more appropriate when dealing with intraspecific genealogies that lie at the phylogeny/tokogeny boundary, i.e., that span the continuum between phylogenetic and population genetic processes [24]. Networks are intended to display in a single graph a generalization of the different phylogenetic trees that can be obtained from the data when character conflict exists on the definition of the genealogical pathways that should connect the samples due to the reticulation process. In consequence, these methods are useful exploratory tools for visualizing data. Yet, there are two potential biological interpretation of such networks: they can represent character-state evolution where relationships between ancestors and descendants are non-dichotomous (due, for example, to introgressive hybridization, in which case the network represents a hypothesis of the true phylogenetic history, e.g., reticulate networks), or they can portrait the uncertainty due to incompatibilities within the data set (and not all the nodes and branches would necessarily represent ancestors and evolutionary events, e.g., split networks) [101, 103]. Networks can be based on distance measures or character states [24, 101]; they can also be built from trees obtained from different data sets (i.e., consensus networks [104]). Belonging to this class of methods, haplotype networks based on organelle data (cpDNA, mtDNA) have been widely used in phylogeographic analyses, but it seems that, in general, network methods applied to nuclear data (such as fingerprinting with AFLPs) have not been fully exploited in the research for the origin and evolutionary patterns of domesticated species.

Additionally, nonhierarchical clustering methods (e.g., PCoA) that do not require assumptions about the underlying distribution of data or mutation models of gene evolution have been suggested as a useful approach for identifying the genetic relatedness of samples in the presence of introgression because, in the presence of reticulate processes, genetic distance measures may be a better indicator of the relationships among individuals than synapomorphy [102]. Assignment methods represent as well an interesting approach for the analysis of data that have been subject to reticulation processes, with similar results to those obtained by network and PCoA methods (e.g., [105]).

New Tools

As with many studies dealing with the history of organisms, phylogeographic analyses are being enriched by different disciplines and approaches. The explicit incorporation of the geographical dimension of population evolution has been particularly signaled as an important condition for future studies, which should complement the (relatively) well developed demographic/phylogenetic methods of the phylogeographic field. Ecological niche and dispersion models associated to Geographic Information Systems (GIS) have been proposed as useful tools for reconstructing past species distribution, which can then be compared to present-day phylogeographical patterns [106–108]. Such geographical models can also be used for proposing hypothesis that can subsequently be tested using statistical phylogeography [109, 110]. On the other hand, phylogenetic spatial diffusion models represent another approach where GIS play an important role. These models treat the geographical locations of a group of sequences as a trait in the organism's phylogeny, and intend to reconstruct where and when the direct ancestors of that sample existed, whether by means of heuristic approaches such as parsimony, or by using probabilistic methods such as maximum likelihood and Bayesian statistics [65].

Additional proposals on the study of the geographical origins of crops are associated to the study of domestication genes, i.e., those genes that are responsible for the traits that define the "domestication syndrome" of the species (e.g., tough rachis, apical growth). The comparison of the phylogeographical affinities between domestication genes and neutral loci (from nucleus and organelles) can reveal the geographical and temporal dynamics of the domestication process and the composite origins of a given crop [98]. For example, domestication genes shared by different lines can be of recent origin while their non-recombining chloroplasts or neutral nuclear genes can be highly divergent, revealing that they are the product of selection from different wild sources followed by hybridization and selective breeding [83, 92]. Nevertheless, it is important to point out that the analysis of the phylogeographic affinities of domestication genes has been proposed in the context of annual plants (e.g., *Triticum*), whose domestication traits have been commonly identified to have a monogenic basis [2, 80, 83]. The traits that characterize domesticated long-lived perennials, in contrast, have been documented to be regulated by more than one gene [111], making this approach less feasible for the study of their history.

Phylogeography of Domestication in Long-Lived Perennial Plants (Trees)

Annual plants constitute the main study system of domestication because of their close association to agriculture, with two families, Poaceae and Fabaceae, including one third of the world's domesticated plants [112]. Their short life cycles, relatively small amounts of gene flow (some species, such as wheat *Triticum aestivum* and lentils *Lens culinaris*, are capable of self-pollination), and high structure among populations [113] favor artificial selection and their isolation from wild relatives, facilitating their domestication. Still, a high diversity of perennial plants from a wide number of botanical families has also been domesticated in different regions of the world. Perennial plant domestication represents a challenge because these plants have long life cycles and exogamous reproductive systems that favor high amounts of intra and interspecific gene flow, which in turn are associated to high levels of inbreeding depression and populational genetic diversity [114]. Because of their long life cycles where fewer sexual generations occur in a given period of time, trees were generally domesticated at a slower rate than annual plants and exhibit fewer domestication syndrome traits [2, 115]. Together with their biological characteristics contrasting with those of annual plants, trees are interesting study systems for the analysis of domestication processes by the diversity of their reproductive strategies, which include sexual and asexual reproduction, their various evolutionary origins reflected in the range of botanical families and orders they belong to, and the ecological setting where they are found, from arid zones to humid tropical forests and temperate regions.

Among their characteristic features, three aspects outstand as directly affecting the evolutionary patterns of trees under domestication: a long juvenile phase, remarkably high levels of gene flow, and low genetic population structure. When natural colonization processes occur, the delayed maturity of trees allows for the arrival of new founders before the first individuals start to reproduce, decreasing the founder effect. In contrast, annual plants that reproduce the first year can quickly fill the available space with their offspring. In this sense, delayed reproduction acts as a key factor (even more important than overlapping generations) in reducing the effects of the domestication bottleneck, maintaining high diversity and low differentiation levels among populations of trees [116]. Another factor contributing to their genetic diversity and low structuring is their mating system (i.e., outcrossing) which increases pollen flow over long distances and reduces genetic drift [117].

Since their levels of pollen flow lead to a highly heterozygous progeny and character segregation, the asexual reproduction of selected individuals has been pointed out as the main strategy allowing for the domestication of woody long-lived perennials in the Old World (Fig. 13.1a) [118, 119]. Indeed, more than 75 % of domesticated perennial fruit crops in the world are clonally propagated [111], a strategy that sidesteps the genetic segregation in the progeny and reduces the time for fruit production. It has been signaled as well that the two historical waves of tree domestication, around 4000 and 3000–2000 years ago, were related to the development of vegetative propagation strategies [115].

The first consequence of the adoption of clonal propagation is that the juvenile phase length that characterizes the natural life cycle of trees becomes greatly reduced, and the founder effects are no longer buffered. Additionally, many propagules can be obtained from one individual in a small period of time in such a way that one genotype can quickly be dispersed, preventing the incorporation of new genotypes to the domesticated pool, just as in a short-lived plant. On the other hand, in order to ensure fruit production of clonally propagated trees despite their autoincompatibility systems, it has been necessary to select individuals with higher rates of autocompatibility (plums, almond), hermaphroditism and monoecy (in the case of naturally dioic species as grape), or parthenocarpy (pear, fig) [119]. Taken together, clonal propagation and autogamous breeding systems are expected to produce lower amounts of gene flow and greater levels of genetic drift, leading to a higher differentiation among populations in domesticated perennial species.

From a long-term evolutionary perspective, selection and vegetative reproduction of high-quality individuals (described as an act of *automatic domestication* [119]) signify that cultivars of clonally propagated species are not true lineages, but clonal replicates of exceptional individuals [120]. This would mean that they have experienced a small number of reproductive cycles since they were brought into cultivation, a strong reduction of genetic diversity and a small divergence from their wild progenitors (Fig. 13.1a) [119]. With the generation of a stronger founder signal and the increasing population differentiation among clonal lineages, the adoption of asexual reproduction should make things easier for the identification of dispersal routes and centers of origin, even in the presence of a low structuration among wild populations.

However, it is worth noticing that there also are tree species that have been domesticated albeit their reproduction by seeds, especially in Mesoamerica and the Amazonian region. It has been proposed that fruit tree domestication can be achieved through the gradual transformation of the composition and structure of forests, from slightly modified forests where valued species are stimulated and non-valued species are removed, to human-controlled environments where tree crops entirely adapted (selected) for particular uses are incorporated [121]. Between these two ends, intermediate agroforestry systems can be identified where trees are currently being domesticated [122]. Among them, swidden agriculture has been proposed as an efficient setting for seed-propagated tree domestication as it favors small population sizes (promoting genetic drift and inbreeding), prevents overlapping generations, and keeps the plot isolated from wild populations [123]. It has been proposed as well that seed-propagated tree domestication is the product of the elimination of undesired trees, together with the cultivation of high-quality individuals and the subsequent selling of their fruits in markets, something that promotes the dispersal of their genotypes [124].

In these species, higher levels of gene flow among individuals and populations due to pollen and seed dispersal are expected to produce higher amounts of genetic diversity inside populations and a lesser structuring between them, together with a higher degree of interspecific hybridization with wild relatives (Fig. 13.1b). Their long juvenile phase and larger population sizes would allow, just as in wild populations, a mitigated founder effect. In the long term, propagation through seeds means that these species have experienced a higher number of reproductive cycles since the first stages of human selection. As a whole, reticulate processes associated to gene flow, the loss of alleles shared with the original progenitor due to successive backcrossing events, the low structuring between populations, and larger population sizes that favor incomplete lineage sorting make the reconstruction of historical relationships between populations a difficult task. Still, differences can be found between species according to pollination ecology and seed dispersal syndromes.

Whether individuals have been clonally or sexually propagated, chloroplast data are particularly useful for tracking the phylogeographic history of domesticated tree species because, being maternally inherited, cpDNA can reveal the genetic affinities between populations. Analysis based on nDNA are also useful for assessing the degree of reduction of genetic diversity due to the domestication bottleneck and for revealing if there have been introgression events with other domesticated pools or with wild relatives (Fig. 13.1). Yet, interpretation of organelle or nuclear genes sharing between domesticated and wild pools is not straightforward mainly due to the difficulty of distinguishing introgression from ancestral polymorphism retention [125]. In the presence of clonal propagation, it is expected that the domestication bottleneck will affect in a similar way both nuclear and organelle loci, while with seed propagation, diversity at organelle loci is expected to be more severely reduced (due to their smaller effective size) than nuclear loci.

In this section, we will portray a brief overview of the genetic and phylogeographic patterns found in selected domesticated tree species with contrasting reproductive and ecological characteristics. We have chosen, as representatives of the clonal propagation strategy: olive (*Olea europaea* L.), date palm (*Phoenix dactylifera* L.), fig (*Ficus carica* L.), apple (*Malus domestica* Borkh.), all from the Old World, as well as ciruela (*Spondias purpurea* L.) from Mesoamerica. As representatives of the seed propagation strategy: coconut (*Cocos nucifera* L.) from the tropical areas of the world, as well as pejibaye (*Bactris gasipaes* Kunth), cacao (*Theobroma cacao* L.), and avocado (*Persea Americana* Mill.) from the Amazonian region and Mesoamerica. We have organized the information regarding their evolution under domestication on three main topics: levels of genetic variation and structuring between populations; identification of centers of origin and, accordingly, dispersal routes to other geographical areas; and contribution of wild relatives to the domesticated pool through introgression events. By reviewing the methods followed by those who have looked for their origins, it is also our purpose to provide a general outlook on the data analysis strategies of this dynamic and diversifying field.

Genetic Diversity and Structure

On their review regarding the consequences of domestication on genetic diversity, morphology and reproductive system of perennial fruit crops, Miller and Gross [111] found that domesticated tree species have undergone a limited reduction of genetic variation, keeping more than 60 % of the genetic diversity found in their wild parents, even exceeding it in some cases (up to almost 130 % in the case of *Leucaena esculenta* [126]). Data from our set of domesticated trees are in accordance with these estimates (Table 13.2), suggesting that their genetic variation has undergone a weak bottleneck. Even in such cases where the wild parent is unknown or has not been studied, which prevents direct comparisons, domesticated trees show levels of variation that correspond to those observed in wild long-lived perennial species with outcrossing mating systems (based on allozymes, observed

Table 13.2 Main characteristics of ten selected perennial species domesticated in the Old and New Worlds

<table>
<tr><th>Species (family)</th><th>Propagation[a]</th><th>Mating system[b]</th><th>Pollination syndrome</th><th>Age at maturity (years)</th><th>Intraspecific domesticated diversity</th><th>Genetic diversity compared to wild parent (marker)</th><th>Cultivated pool structuring [wild pool structuring] (marker)</th><th>Refs.</th></tr>
<tr><td rowspan="2"><i>Olea europaea</i> L. subsp. <i>europaea</i> (Oleaceae)</td><td>V</td><td>Andromonoecy, self-compatible to self-infertile</td><td>Wind</td><td>5–6</td><td>~1200 recognized cultivars for the obtention of oil or olives</td><td>57.5–64 % (isozymes)</td><td>$D = 0.50–0.93$ [0.51–0.87] (AFLPs)</td><td rowspan="2">[119, 132, 148, 154–160]</td></tr>
<tr><td colspan="7"><i>Main genetic and phylogeographic patterns</i>: Differentiation among Western and Eastern Mediterranean Basin in cpDNA and mtDNA reveals selection of cultivars in the Near East followed by their dispersion to the West, as well as selection of germplasm of Western origin. Nuclear differentiation retains the East–west cline of wild populations and reveals affinities between cultivars and local wild forms, generated whether by local selection or by posterior hybridization with introduced cultivars</td></tr>
<tr><td rowspan="3"><i>Vitis vinifera</i> L. subsp. <i>sativa</i> (Vitaceae)</td><td rowspan="2">V</td><td>D (silv)</td><td rowspan="2">Wind, autopollination</td><td rowspan="2">3</td><td rowspan="2">~5000 cultivars destined to wine, raisin, or table grape production</td><td rowspan="2">69–132 % (SSRs)</td><td>$D = 0.769$ [0.684]</td><td rowspan="3">[119, 127, 128, 131, 141, 142, 161–164]</td></tr>
<tr><td>H, A (dom)</td><td>Gst = 0.353 [0.169] (cpDNA SSRs)</td></tr>
<tr><td colspan="7"><i>Main genetic and phylogeographic patterns</i>: Originated in the Near East, especially the genetically diverse Caucasus, cultivated grapevine was dispersed toward the West with the “wine culture.” Organelle and nuclear data suggest gene flow between eastern cultivars and western wild grapevines, with local selection events giving rise to Western cultivars, especially in the Iberian Peninsula and Italy which represent glacial refugia. Pedigree relationships have revealed crosses among elite cultivars and the diversification of cultivar families already documented in historical sources, together with a differentiation linked to fruit uses (wine/table grapes)</td></tr>
</table>

(continued)

Table 13.2 (continued)

Species (family)	Propagation[a]	Mating system[b]	Pollination syndrome	Age at maturity (years)	Intraspecific domesticated diversity	Genetic diversity compared to wild parent (marker)	Cultivated pool structuring [wild pool structuring] (marker)	Refs.
Ficus carica L. (Moraceae)	V	D	Parthenocarpy (dom) Wasps (wild, dom)	2–4	~700 cultivars	Ho = 0.44–0.55 (SSRs) in cultivated varieties	Fst = 0.031–0.164	[119, 133, 143, 165–169]
	Main genetic and phylogeographic patterns: Probably originated in Transcaucasia and the Middle East, it was dispersed to the south and west. Three main wild gene pools predating domestication have been identified based on mtDNA: Balearic, East and West Mediterranean, with probable introgression among East and West populations due to human activities. Based on nuclear markers, cultivars (i.e., female trees) show complex relationships, with a weak genetic structure and mixed ancestry that lack the traces of colonization processes or of their geographic origin. At a local scale, old varieties coexist with more recent cultivars produced by hybridization with native wild male trees and, to a minor extent, by somatic mutations							
Phoenix dactylifera L. (Arecaceae)	V, S	D	Wind, bees (wild, dom) Manual (dom)	6–10 S 4–5 V	~5000 (female), classified as dry, semidry and soft	Ho = 0.81–0.99 (SSRs) in cultivated varieties		[119, 134, 149, 150, 165, 170, 171]
	Main genetic and phylogeographic patterns: Its wild progenitor remains unknown. Based on historical evidences, it was probably domesticated in the Persian Gulf region and later dispersed to North Africa. Nuclear markers have shown high levels of diversity and low levels of structuration, with genetic variability maintained locally within populations. Female cultivars show complex relationships, and are independently related to different male varieties							

Malus domestica Borkh. (Rosaceae)		I	Insects		7000 cultivars	105–108 %, SSRs		[95, 125, 172–178]
	Main genetic and phylogeographic patterns: Based on morphological and cpDNA data, it has been recognized that apple was first domesticated from wild *M. sieversii* in Central Asia. Once introduced to Europe by Greeks and Romans, wild European *M. sylvestris* contributed to the domesticated genetic pool, as revealed by chloroplast and nuclear genetic analyses. However, relationships among cultivars are not well resolved according to pedigree, geographical origin nor kind of use (cider vs. dessert apples), probably due to the common occurrence of inter and intraspecific hybridization							
Cocos nucifera L. (Arecaceae)	S	M	Insects	~600 varieties	Two main forms: self-pollinating dwarf with “niu kafa” oblong fruits and cross-pollinated tall with “niu vai” rounded fruit		Fst = 0.233 (SSRs)	[138, 179–186]
	Main genetic and phylogeographic patterns: Morphological diversity, local names, diversity of its uses, and genetic variation suggest an origin in Southwest Asia, particularly the Malesian region, from where it was dispersed by ocean currents and human populations westward to the Indian Ocean and Africa, and eastward to America. Historical data and genetic analyses have confirmed that coconuts from the West and East coasts of the American continent have originated from introductions from the Philippines and Africa (via the Caribbean region), respectively. Although wild populations can be found in the Pacific islands and Central America, most populations include domesticate types or introgressed forms. Genetic markers have confirmed the distinction among tall and dwarf types							

(continued)

Table 13.2 (continued)

Species (family)	Propagation^{a}	Mating system^{b}	Pollination syndrome	Age at maturity (years)	Intraspecific domesticated diversity	Genetic diversity compared to wild parent (marker)	Cultivated pool structuring [wild pool structuring] (marker)	Refs.
Bactris gasipaes Kunth var. *gasipaes* (Arecaceae)	S	M, protogynous	Beetles, gravity and wind	5–7	16 landraces	93–116 % (RAPDs, SSRs)		[123, 186–191]
	Main genetic and phylogeographic patterns: Probably domesticated in southwestern Amazon, where the greater diversity of landraces is found. Based on floral characters and a cline of nuclear genetic diversity, it has been proposed that the palm was later dispersed to the northwest and Central America. However, other authors argue for multiple domestications within the species range based on fruit morphology and nuclear SSRs. Genetic closeness between cultivated and local wild palms has been interpreted by some as an indicator of gene flow, while others consider it as a trace of independent selection events							
	Low differentiation among populations (12–15 %) and high within-population diversity. Nuclear markers have shown isolation by distance at a regional scale and significant gene flow at a local scale, following a metapopulation model linked to trade routes							
	Nuclear markers have also revealed inbreeding at a local scale and in varieties selected for spinelessness							
Persea americana Mill. (Lauraceae)	S	H, DS	Bees and other flying insects	5–7	Three races/ botanical varieties	80–91 % (nucleotide diversity)		[140, 166, 192–197]
	Main genetic and phylogeographic patterns: Races correspond to geographical ecotypes that were domesticated independently (highland Mexico, highland Guatemala, and lowland Guatemala to Costa Rica). Races remain as distinct groups with nuclear markers, but many modern cultivars show hybrid (interracial) origins. Molecular markers have helped to identify the racial profile of the pollen donor of hybrid cultivars and to reclassify them							

<table>
<tr><td rowspan="2"><i>Theobroma cacao</i> L. (Sterculiaceae)</td><td>S</td><td>H, I</td><td>Moths, ants</td><td></td><td>Three morpho-geographical varieties (subspecies) (Criollo [Central America], Forastero [Upper and Lower Amazon], and Trinitario [hybrid of the other two])</td><td></td><td></td><td rowspan="2">[135, 197–202]</td></tr>
<tr><td colspan="7"><i>Main genetic and phylogeographic patterns</i>: Nuclear and morphological data show Upper Amazonia (eastern flank of Andes in Peru, Ecuador and Colombia) as a center of diversity and possibly a center of origin. High homozygosity levels and low diversity in Criollo from Central America supports as well an origin in South America, from where cacao may have been spread by man northward to the South of Mexico. On the other hand, nuclear and uniparental markers show a clear discrimination between Criollo and Forastero types, suggesting that they diverged independently on both sides of the Andean barrier. Additional linguistic evidence suggests a northern origin (Central America), from where the primitive variety that gave rise to domesticated cacao may have disappeared</td></tr>
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(continued)

Table 13.2 (continued)

Species (family)	Propagation[a]	Mating system[b]	Pollination syndrome	Age at maturity (years)	Intraspecific domesticated diversity	Genetic diversity compared to wild parent (marker)	Cultivated pool structuring [wild pool structuring] (marker)	Refs.
Spondias purpurea L. (Anacardiaceae)	V	Polygamo-dioecious	Insects		Variation in fruit color, size, texture and taste	90 %, AFLPs	θst = 0.398 (wild = 0.302)	[137, 139, 203]
	Main genetic and phylogeographic patterns: At least two origins have been proposed for this species based on uniparental markers: western central Mexico and Central America. High diversity and unique haplotypes in cultivated populations suggest that agricultural habitats act as reservoirs of genetic variation. Ongoing hybridization or incomplete lineage sorting with *S. mombin*							

[a] *V* Vegetative, *S* Seeds

[b] *H* Hermaphrodite, *HD* Hermaphrodite dicogamous, *D* Dioecy, *M* Monoecy, *DS* Dicogamous synchronized, *A* Autocompatible, *I* Autoincompatible, *AFLPs* amplified fragment length polymorphisms, *SSRs* simple sequence repeats, *RAPDs* randomly amplified fragment length polymorphisms, *D* Nei's genetic distance [204], *Ho* observed heterozygosity, *Fst* Wright's population differentiation index [205], *θst* Stewart and Excoffier population genetic differentiation index [206]

heterozygosity Ho = 0.180) and with animal-propagated seeds (Ho = 0.225) [113]. Interestingly, clonally propagated species do not show lesser amounts of diversity when compared to seed-propagated ones. Even European grape, which suffered from a dramatic reduction in cultivar diversity due to mildew diseases and phylloxera in the second half of the nineteenth century, does not show evidences of additional bottlenecks [127].

In contrast, the distribution of this diversity among populations of wild and domesticated status shows clear differences between species. For example among clonally propagated species, domesticated grape and ciruela show a slightly higher structuring among populations than their wild counterparts, while cultivated olive has similar levels of structuring when compared to wild oleaster populations. On the other side, clonally propagated fig presents a surprisingly low proportion of genetic variance among domesticated populations. The expectation of a stronger genetic structure due to increased levels of genetic drift associated to vegetative propagation is therefore not observed in most of the cases. Moreover, species that have been cultivated through cuttings and those propagated through seeds do not seem to contrast as much as expected due to their mode of propagation. What causes, additional to the biological characteristics of perennial plants already described, can be identified to account for the high genetic diversity and moderate levels of genetic structuring observed in the species revised?

Mating system can be signaled as an important factor in the cases of fig and date palm, which are clonally propagated species with very low levels of genetic structuring. Fig and date palm are dioecious, making necessary to plant, next to fruit-producing female individuals, pollen-producing males in order to bear fruit (although there also are parthenocarpic fig varieties). By enhancing the planting of more than one variety in the same plot, dioecy propitiates gene flow among cultivated individuals, and between cultivated and wild plants, producing genetically variable offspring that can be incorporated to the domesticated pool (see next section about introgression).

However, intraspecific diversity, expressed in a great number of cultivars and local forms, is probably the most striking aspect shared by the perennial species shown in Table 13.2. From an unknown number of varieties distinguished by their different fruit size, color, and flavor in *Spondias purpurea* to the 5000–8000 formally described grape varieties, domesticated perennial species have been the object of distinct selection pressures in order to fulfill local gastronomic and aesthetic preferences, as well as for adapting cultivars to particular environmental conditions. The occurrence and selection of somatic mutations has been pointed out as an important mechanism behind the diversification of some cultivar groups or families [128–130]. Still, somatic mutations cannot account for all of the intraspecific diversity observed in domesticated perennial species. It is more likely that such diversity is the product of several selection events, whether from separate and independent wild sources (in which case every cultivar is a different clone isolated from the others because of vegetative propagation) or from the available cultivated diversity (and a given cultivar can result from the crossing between two previously existing cultivars, or between a cultivar and a wild parent). This would mean that domesticated perennial species retain high levels of genetic diversity and a moderate structuring due in large measure to successive events of human selection that propitiate the incorporation of different genetic variants to the domesticated pool, and to the presence of intra and interspecific hybridization among cultivars, and between cultivars and their wild parents.

Centers of Origin and Geographical Dispersal

The study of phylogeographic data provides interesting insights into the history of each perennial species and allows for the identification of patterns that shed light on the processes that characterize the domestication of trees as a whole. On one hand, the geographical distribution and relative frequency of organelle genetic variants (haplotypes) in populations and cultivar collections has been the main tool for the identification of dispersal routes of domesticated varieties, and, at the same time, for the location of their center of origin. This has been the case in olive and grape, probably the most studied domesticated perennial species, which share a pattern of East to West dispersal in the Mediterranean Basin, from the Near East up to Portugal (references in Table 13.2). The existence of a genetic structure in wild populations that predates their domestication has been most useful for the identification of such processes; it harbors great relevance as well for the design of conservation strategies oriented to safeguard genetic resources destined to breeding strategies [131, 132]. However, in some cases, the domesticated lineage has not kept the trace of the structure observed in wild populations, hindering the reconstruction of its geographical history, as it is the case of fig [133]; this can be caused by hybridization among cultivars, which creates reticulate relationships among nuclear loci, and by their dispersal to different regions, which propitiates gene flow and entangle haplotypes from different areas. In other cases, the absence of a wild progenitor to be included in genetic analyses has hindered the interpretation of phylogeographic patterns and the identification of a putative center of domestication, as in date palm, which is found only as a cultivated plant or in anthropogenic areas [134]. Nevertheless, dispersal routes and the center of origin have not been easy to identify in certain cases mainly due to a lack of appropriate data, particularly from organelle loci. In cases such as pejibaye and cacao, cultivated pools have been found nested within different wild populations, either suggesting that wild and domesticated populations have exchanged genetic material (i.e., hybridization) or that domestication has occurred more than once. These two scenarios could be differentiated if organelle data were compared to nuclear patterns, but in the absence of cpDNA or mtDNA analyses, dispersal has been deduced to occur from the most genetically (based on nuclear data) and/or morphologically diverse area toward other regions where the domesticated species is found, following Vavilov's principles. But, as expected, debate takes place in the presence of biological and historical evidence in favor of contrasting hypothesis (as in cacao [135, 136]).

Overall, the cases described in Table 13.2 show that there exist a range of situations on the information about the history of domesticated perennial species that can be retrieved from genetic data. Clearly structured genetic patterns from nuclear and organelle loci have allowed for the recognition of the Eastern Mediterranean Basin as the geographical origin of olive and grape, from where germplasm was dispersed to other areas whose local wild populations contributed to the domesticated gene pool (e.g., Italy, Spain). Data therefore suggest a single origin for these species, although the presence of western organelle haplotypes with admixed nuclear alleles can also suggest domestication of western populations, followed by hybridization with introduced Eastern cultivars, which would mean multiple origins for these crops. A clear geographical pattern of mtDNA has also revealed at least two domestication events in the case of ciruela [137]. In contrast, most of the perennial species revised display complex patterns and/or have been studied with less detail, making difficult to pinpoint their center of origin and to know if they have been taken into cultivation one or more times [111]. Complex relationships lacking a geographical arrangement among cultivars have revealed an intricate history of human selection, dispersion, and gene flow in the case of dioecious date palm and fig. Albeit being reproduced through cuttings, olive, grape, fig, and date palm show contrasting genetic and phylogeographic patterns, due to their different mating systems as well as different particular histories (Table 13.2). Tropical species propagated by seeds as cacao and pejibaye show an intermediate situation: they display interesting patterns of geographically structured genetic diversity, but these have been interpreted in contrasting ways. Complex relationships among coconut cultivars due to its long history of human management combined with its high capacity of water dispersal have also hampered the reconstruction of its domestication history at a regional scale, although the main patterns of its dispersal have been elucidated at the world scale [138]. In these three tropical species, whose history has been studied through nuclear markers only (Box 1), additional organelle data should help to identify their closer wild parents and to clarify their dispersal routes. Finally, although the main genetic pools of ciruela and avocado have been identified in Mexico and Central America [137, 139, 140], little is known about the history of their dispersal and domestication at a local scale. In the case of avocado, most studies have dealt with the origins of cultivars developed in the last two centuries from the main three avocado races, but the history of each race within its original area of distribution together with the historical relationships among these races predating modern breeding efforts remain to be addressed.

Box 1: On the Methods Used for Studying the Phylogeography of Domesticated Perennial Species

A brief overview of the methods employed in the literature on ten selected perennial species (Fig. 13.5) shows that most of these studies have relied on nuclear markers. Amplified fragment length polymorphisms (AFLPs) are recognized as a useful and reliable anonymous marker [29] and have been used in a variety of species such as olive, fig, date palm, coconut, pejibaye and ciruela. Simple sequence repeats (SSRs or microsatellites) have been widely

(continued)

Box 1 (continued)

used in the last decade and seem to be the marker of choice for future studies. In contrast, nuclear sequences have been used in a more limited extent. Surprisingly, there exists an important lack of data from uniparental markers in species such as avocado, pejibaye, coconut and fig. As for their statistical methods, they share similar approaches, mostly from descriptive phylogeography. Basic aspects of genetic data are displayed mainly by means of population genetic descriptors and analysis of molecular variance (AMOVA). Principal Coordinate Analysis (PCoA) is also a common approach, used in many studies next to clustering methods (UPGMA, NJ and parsimony trees) in order to contrast both non hierarchical and hierarchical approaches. Assignation methods have also been used in more recent studies and, as such, they will probably be used with more frequency in the future, especially when dealing with nuclear microsatellite data. Surprisingly, NCPA has seldom been used in these studies (only one example in ciruela [137]) even during the decades when it was more widely used. Network approaches were seldom used in the studies revised, even when low bootstrap values in clustering methods were recognized by the authors as suggesting hybridization (for example in avocado and cacao [195, 201]). Finally, statistical phylogeography tools are not found among the sampled studies, excepting the analysis by Gunn et al. [138] in apple, who applied Approximate Bayesian Computation methods (ABC). This suggests that statistical phylogeography and coalescent analyses are starting to be used at a very slow pace. This can be explained, on one hand, by the fact that many of the studies are based on a population genetic perspective, dealing with a small number of populations at a time, commonly at a regional scale. They focus on the amounts and direction of gene flow among populations at an ecological timescale, and do not necessarily include an historical perspective. Nevertheless, population genetic studies have provided interesting data regarding introgression levels with wild relatives and among cultivars, and undoubtedly complement phylogeographic analyses of deeper timescales and wider geographical scope. On the other hand, many studies rely on the analysis of a small number of accessions from germplasm collections that do not allow for a population perspective on data analysis, even when samples from wild parents are included for analyzing clustering patterns. The analysis of relatedness and hybridization among domesticated lines and with their wild relatives based on germplasm collection samples have also been signaled as a limited approach for unraveling historical relationships, since a small number of individuals cannot be representative of a given variety or cultivar when there exists a high degree of naturally occurring gene flow, as in seed propagated outcrossing species [185]

Introgression from Wild Parents

The comparison of nuclear and organelle markers has also allowed for the identification of introgression events with wild populations in different areas of the current distribution of many domesticated tree species. The detection of domesticated individuals or cultivars harboring haplotypes that are characteristic of sympatric wild populations suggests that wild plants were pollinated by domesticated forms and, subsequently, the resulting seeds were incorporated into the cultivated pool. This phenomenon has been identified in grape [141], where gene flow from cultivated forms into wild populations has been calculated to be from 4.2 to 26 % [142]. The pollination of domesticated individuals by wild pollen has also been documented in those cases where a given cultivar shares its cpDNA or mtDNA haplotype with other domesticated forms, but harbors nuclear alleles present in sympatric wild populations. In cases where organelle data are not available, the composite nature of hybrid cultivars or individuals has been detected through multivariate approximations, assignment methods, and pedigree analysis, as in apple, ciruela, apple, and avocado (refs. in Table 13.2). The high degree of phylogeographic blurring and complex relationships between female cultivars in dioecious species (fig and date palm) is most probably due to hybridization events. As previously mentioned, the almost essential presence of male individuals needed for pollination and fruit production has opened the door to pollen-mediated gene flow from wild populations into the domesticated pool, leading to the development of new local cultivars, as it has been documented in fig from Morocco [143].

As a whole, these evidences are in agreement with the already well-known potential of trees for intraspecific (e.g., olive, grape, fig, coconut, date palm, and avocado) and interspecific gene flow (e.g., ciruela and apple). More importantly, these data show that seeds, which contain the new genetic variants produced by cross-pollination, have significantly contributed to the evolution of domesticated tree populations, even in those species that have been traditionally propagated through cuttings in the Old World. This phenomenon also accounts for their high levels of genetic diversity, as tree species with both sexual and asexual modes of reproduction may maintain higher levels of genetic variation [144].

Toward Richer Models of Evolution of Domesticated Perennial Species

The incorporation of new genetic variants through seedling selection and the multiple selection of cultivars in different geographical areas reflects that the domestication of tree species (whether through cuttings or seeds) was not a rapid transition that occurred in a single area. On the contrary, genetic and phylogeographic patterns strongly suggest that the current composition of these species is the product of a range of processes including (1) more than one starting point where some wild individuals were originally selected, (2) the dispersal of this primary domesticated pool to other areas, and (3) the subsequent incorporation of new variants produced by cross-pollination among selected pools and between domesticates and local wild parents, which acted as female and male donors. Interestingly, this dynamic process seems to hold equally well for clonally and seed-propagated species, as well as those distributed in temperate and tropical regions.

On one hand, this means that both nuclear and organelle data are needed for identifying routes of dispersal and patterns of gene flow. It means as well that it is necessary to enlarge our analytical toolkit with more powerful and adequate methods (see Box 1) in order to disentangle the complex genetic relationships among cultivars and populations. On the other hand, such a multifaceted scenario requires a closer collaboration between genetics and other disciplines such as ethnobotany for interpreting data, as well as for formulating new hypothesis and models (Fig. 13.2).

For example, a main issue where ethnobotany can play an important role is on the analysis of the mechanisms that are responsible for the incorporation of spontaneous hybrid seedlings to domesticated pools [145]. Fruit trade, followed by the sowing of the seeds contained in them, has undoubtedly acted as an important mechanism for the geographical dispersal of domesticates, as well as for the development of cross-bred individuals and, eventually, new varieties. Fruits are the main plant part selected in most tree species and are commonly transported to other regions for selling, away from their original area of cultivation. Although differences exist regarding the distance fruits can travel and the longevity of seeds within them (dates and coconuts are more easily transported than figs or avocados, for example), seeds are more resistant than clonal cuttings for such kind of journeys. Once made available in a new region, fruits can be acquired by a farmer that finds them appealing; he will then sow the seeds in order to have such an interesting variety in his orchard. Johannessen [146] documented this kind of process in the Amazonian region, where growers acquire high quality fruits of pejibaye palms from family members, friends, and local markets for their own plantations, and then select the better individuals, leading to the incorporation of introgressed individuals into the domesticated gene pool, which then becomes more diverse [123].

Aguirre-Dugua et al. [147] documented the transportation and cultivation of seeds and cuttings of preferred varieties of the gourd tree (*Crescentia cujete*, Bignoniaceae) among Maya communities, which is in accordance with the genetic and morphological differentiation found between homegarden and wild populations; tolerance of spontaneous individuals harboring wild haplotypes and intermediate fruit morphologies is also in accordance with hybridization processes at a local scale (Fig. 13.3).

Similar evidences exist for the perennial species here reviewed which have been subject to a diverse array of human management practices that can account for genetic traces of hybridization. For example, in the island of Sardinia, domesticated olives are grafted onto wild oleasters [148], a coexistence that should facilitate gene flow when wild shoots develop and flower. In the case of grape and apple, until the

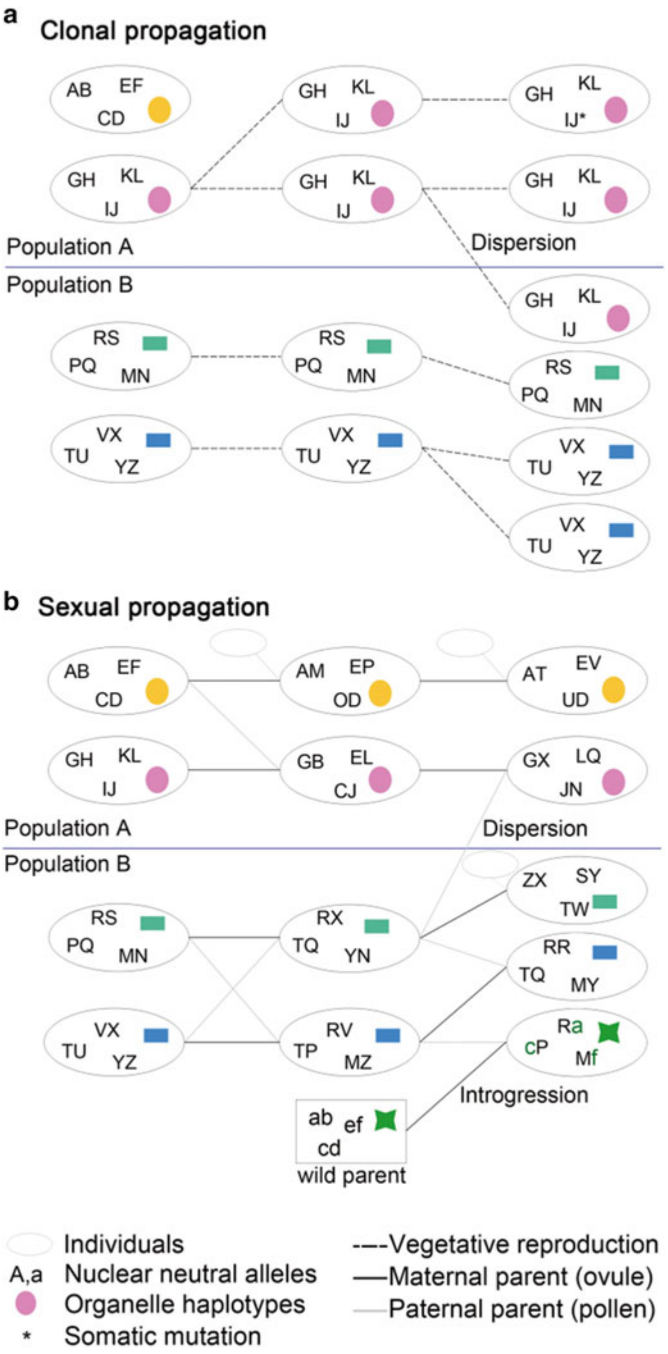

Fig. 13.2 Clonal and sexual propagation generate contrasting genetic outcomes. (**a**) With clonal propagation, individuals retain their nuclear and organelle (mtDNA and cpDNA) genetic constitution, and diversity arises through somatic mutations. (**b**) Sexual propagation leads to new nuclear genetic combinations, while organelle DNA is inherited as a unit (in angiosperms, cpDNA and mtDNA are mainly maternally inherited). Dispersion and introgression events can be detected through nuclear (when foreign pollen and ovules are incorporated to the domesticated pool) and organelle DNA (only when foreign ovules—future seeds—are incorporated)

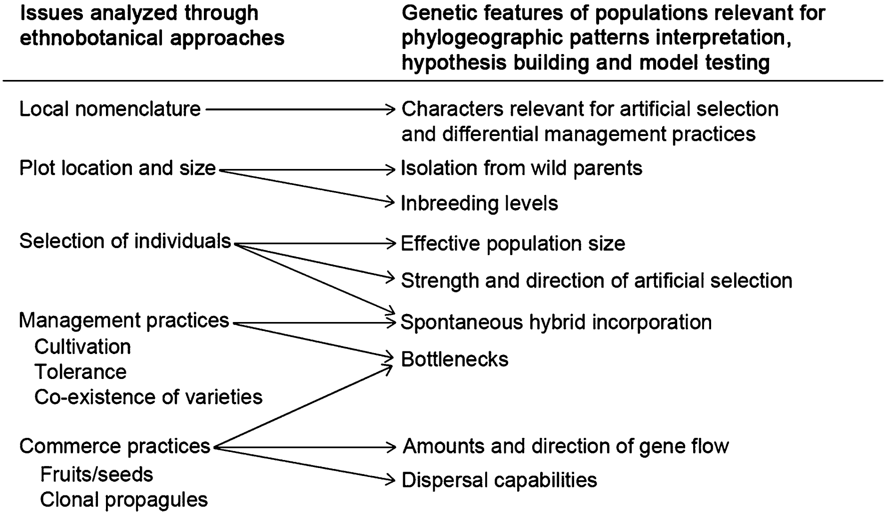

Fig. 13.3 Ethnobotanical studies represent a rich source of information on the genetic dynamics of populations under domestication. Information on human management practices of plant individuals and populations can be useful for interpreting phylogeographic patterns as well as guiding sampling strategies, proposing new hypothesis and testing models on the tempo and mode of tree domestication

twentieth century plantations were constituted by many different varieties, and this likely gave rise to a naturally extensive hybridization [95, 127]. It is also known that common fig, if pollinated, produces better quality fruits than parthenocarpically developed figs [133], something that would favor human selection of sexually reproducing cultivars. It has also been documented that male figs used for pollination are collected and then hanged in the branches of female trees without taking into account their agronomical characteristics, allowing for the usage of any local male individuals [143]. In the case of date, seedlings are commonly grown for commercial propagation in Northern Africa and the Arabian Peninsula, where they receive a special name: “khalt” or “balady” [149]. Male date individuals, in contrast to fig, are strongly selected and used to hand pollinate female palms because of the favorable metaxenic effect of pollen on fruit size and quality [134]; pollen grains are then usually stored and exchanged at a local and regional scale, as it is the case of offshoots, while seed dispersal takes place by travelers and traders across geographical borders [150].

Altogether, the documentation of management processes that involve selection and transportation of individuals, their fruits, seeds and clonal propagules, as well as practices that favor gene flow, are highly useful for interpreting and understanding population genetic data and phylogeographic patterns. Current farmer practices, commonly developed in traditional agroecosystems such as agricultural plots and homegardens, can be used to quantify and model the effects of artificial selection (whether conscious or unconscious) on the effective population size and inbreeding

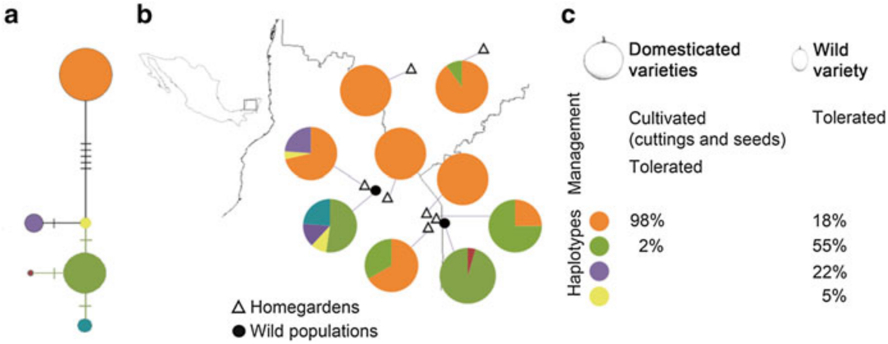

Fig. 13.4 Ethnobotanical information regarding the classification and management of *Crescentia cujete* varieties complements phylogeographic genetic data at a regional scale. (**a**) Median joining haplotype network based on five cpDNA microsatellites, bars representing mutational steps; (**b**) Distribution and frequency of haplotypes in trees from homegardens and wild populations in the Yucatan Peninsula, Mexico; (**c**) Haplotypes found in trees from homegardens (populations marked *triangle* in (b)) recognized by the interviewees as belonging to domesticated and wild varieties based on fruit morphology. Note hybridization evidence (domesticated trees harboring *green* wild haplotype and wild trees with *orange* domesticated haplotype). Haplotype network and genetic data from Aguirre-Dugua et al. [147]

levels of tree populations, as well as for estimating the amounts and direction of gene flow among them. They can be used as “windows to the past” in order to unravel the genetic makeup of perennial species populations under domestication [151]; they also are “windows to the present” where valuable ongoing processes of domestication occur (Fig. 13.2) [1, 152].

Finally, if we consider the proposal of Wiersum [122] on the co-domestication of forests and fruit trees, it is likely that different populations of the same tree species have been simultaneously managed and selected in a wide geographical area, exchanging genes through fruit trade. Agroforestry systems where this management occurs could provide evidence for a protracted model of tree domestication; notwithstanding, they could also display stronger selection pressures and inbreeding dynamics in agreement with a rapid transition to domestication (as in pejibaye [123]). These productive systems, analyzed from complementary genetic and ethnobotanical perspectives, could therefore be used for testing expected genetic patterns under different domestication models and provide new elements for the improvement of current proposals (Fig. 13.4).

Conclusions and Perspectives

Domesticated long-lived perennial plants include a wide array of species with contrasting reproductive systems, ecological characteristics, and forms of propagation. Together with their particular histories, this diversity offers the opportunity to build

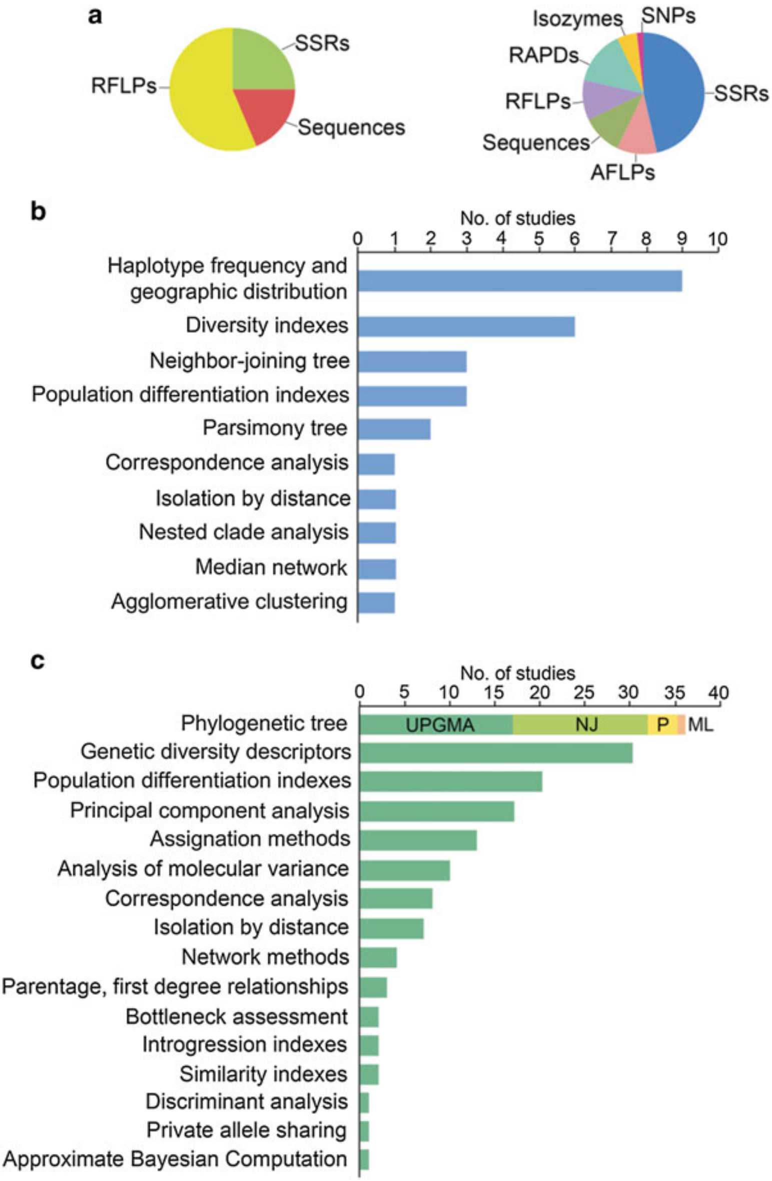

Fig. 13.5 Main methods employed by studies dealing with the history of ten selected domesticated perennial species (species and references in Table 13.2). From all the studies revised ($n = 59$), 8 used only organelle DNA (cpDNA and mtDNA), 45 utilized nuclear DNA, and 6 used both organelle and nuclear DNA. (**a**) Markers employed with organelle DNA (left, $n = 14$ studies) and nuclear DNA (right, $n = 51$). *RFLPs* restriction fragment length polymorphisms, *SSRs* simple sequence repeats or microsatellites, *RAPDs* randomly amplified polymorphic DNA, *AFLPs* amplified fragment length polymorphisms, *SNPs* single nucleotide polymorphisms. (**b**) Number of studies that employed different analytical methods with organelle DNA. (**c**) Number of studies where diverse analytical methods with nuclear DNA were used. *UPGMA* Unweighted Pair Group Method with Arithmetic Mean, *NJ* Neighbor-Joining, *P* Parsimony, *ML* Maximum Likelihood

a more comprehensive theory of plant evolution under domestication; it allows analyzing the relationship between particular features of trees and evolutionary facets such as bottleneck sensitivity, geographical dispersal capabilities, diversification, and hybridization potential.

The majority of the analyses included in the literature revised in the present chapter have used descriptive phylogeographic approaches. Interestingly, despite the risks associated to the overinterpretation of data, descriptive studies using different data sets and methodological tools, from local to regional scales, have obtained consistent results in some widely studied species such as olive and grape. Yet, in other cases as in coconut, date palm, fig, pejibaye, and cacao, the interpretation of genetic patterns has not been straightforward (mainly caused by complex reticulate relationships among populations and/or a lack of appropriate analytical methods) or has supported contrasting hypothesis about their origins. Nevertheless, a general picture emerges from the different phylogeographic, phylogenetic, and population genetic studies developed on domesticated perennial species.

Domesticated perennial species present high genetic diversity levels (supporting the idea of their populations going through a weak bottleneck), dispersal over long distances, hybridization between domesticated pools, and introgression with wild relatives in different areas of their current distribution. Tree domestication consists on a process that spans thousands of years where the initial steps of artificial selection took place in one or sometimes more than one geographical area, ensued by the dispersal of selected pools, the occurrence of gene flow with wild parents and other domesticated lines, and succeeding selection events in posterior historical periods. In this context, the testing of the two traditional opposite hypothesis (a single origin where a limited wild stock was selected at a particular period of time vs. multiple origins with a large number of founders recruited along the distribution range of the wild progenitor) is replaced by the analysis of the assemblage of processes and mechanisms that have taken part in the molding of domesticated perennial plants as we know them today [89, 98]. The search for their precise botanical and geographic origins will remain, nevertheless, an active and important area of interest for academicians, breeders, and conservationists.

The field of phylogeography and its tools (i.e., gene trees and the analysis of the spatial distribution of their branches) are particularly intended for some new promising areas of research on the evolution of domesticated perennial species. Among potential avenues of future inquiry there is, for example, the usage of palaeoclimatic models for estimating the historical distribution of wild parents and the coupling of such distribution with current patterns of genetic relatedness among domesticates and their wild relatives. Was the wild progenitor restricted to a particular area by the end of the Pleistocene or was it abundant and widespread? What is the probability of the domesticated pool having contact with a wild parent in a particular region at a given period of time and the likeliness of an introgression event? Is there any correspondence between the wild parent's historical distribution and the presence of archaeobotanical remains or documentary evidences? Can ancient DNA recovered from archaeobotanical samples [94, 153] be included in the genealogy of present populations?

Gene trees can also be used to address more general questions on perennial species domestication, such as the delimitation of their lineages. Zohary and Spiegel-Roy [118] proposed that clonally propagated trees do not represent true lineages because they are but clonal replicates of high-quality wild individuals and that they have undergone a reduced number of sexual cycles since they were first selected. However, data show that hybridization (and therefore sexual reproduction) has played an important role in the evolution of these species. On the other hand, seed-propagated species present a higher number of generations separating selected and wild individuals, but their important amounts of gene flow should hamper their differentiation. We may therefore ask if domesticated perennial species form true lineages (or a set of lineages) and, if so, which are the main evolutionary forces driving their differentiation (drift, artificial selection, reproductive or geographical isolation, etc.).

Finally, phylogeography can contribute to the natural history of these species and to the conservation of their genetic resources. Links can be drawn between the components of the gene tree and their geographical origin and provenance (i.e., homegarden, plantation, germplasm bank) for portraying a picture on the location of such resources, their diversity, and the genetic makeup of the different productive systems that harbor them. For example, we may ask whether traditional agroecosystems harbor varieties of old or recent origin, of wide or local distribution, of clonal or out-crossing origin [143]. Dioecious species merit special attention due to the differential contribution of male and female individuals, whose respective roles in the domestication process and the distribution of genetic resources have not yet been studied with enough detail. This information is essential in order to propose better conservation strategies coupled with productive practices.

As a whole, it is expected that future studies will enlarge the already available and well-known set of descriptive analytical tools (population genetics descriptors, hierarchical clustering methods, multivariate analysis, and assignation methods) for including tree methods that account for reticulate relationships and the testing of particular phylogenetic and demographic hypothesis through coalescent models under a statistical phylogeographic framework. The sampling of populations, additionally to the usage of individual accessions from germplasm banks, should also help to build a richer picture of their evolution. Collecting wild populations becomes pressing as well because they are commonly under threat [95, 131].

Finally, we hope for a richer exchange between ethnobotany and phylogeography. Documentation and analysis of plant management practices in traditional agroecosystems should provide a necessary frame of reference for interpreting genetic data obtained in phylogeographic studies. Relevant information provided by ethnobotanical studies includes the classification of local varieties, artificial selection practices, incorporation of spontaneous seedlings, management of clonal and sexual propagules, and commerce practices. They can act as a guide on artificial selection pressures, bottleneck events, and gene flow mediated through seeds and pollen that can be useful for outlining better sampling schemes and formulating new questions and models on the processes that lie behind tree domestication.

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Chapter 14

Your Beans of the Last Harvest and the Possible Adoption of Bright Ideas

Daniel G. Debouck

Abstract This review considers which species of beans were domesticated out of a total of 80 or so species in tropical America, and the morpho- and ecological reasons and other nutritional aspects behind the choices of Amerindians who knew and experimented a lot with the flora. It explains why places of domestication refer to the locations where seeds of wild forms were picked for the last time. It further shows the current discrepancies between the archaeological records and the genetic data. The seven domestication events affecting the genus Phaseolus, five in Mesoamerica and two in the Andes, seem to have happened originally outside the presence of maize and before the wide use of ceramics, with food uses possibly different from the ones known nowadays (like toasting). The bright idea by Amerindians was to combine maize and beans into a performant agronomic and nutritional association that diffused so widely in pre-Columbian America and set the basis for the many brilliant civilizations they left us.

Keywords Phaseolus • Amerindians • Crop wild relatives • Phylogeography • Archaeology • Domestication • Founder effect • Maize

Beans! Today to some of us the word evokes well cooked food of the pot in winter [1], to others colorful salads of the summer [2], to fewer who traveled deep into the central Andes an attractive toasted grain [3]. Beans have often been the food of last resort in impoverished suburbs, or on long journeys into the unknown during the nineteenth century, or on ships wandering in stormy seas, because in contrast to many food items they are a highly nutritive and well balanced food that stores well. These two key properties explain their worldwide adoption, well reflected by the numerous vernacular names (some reported by Davidson [4]) [4], and being among food legumes only second to soybean and peanut (both being grown largely for their oil content). Viewing this worldwide adoption into a time and space perspective, it is worth mentioning that large kidney beans were already reported in Italy by 1528

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Table 14.1 Bean crops and some ancient vernacular names (languages classified along [27])

Bean crops	Vernacular names	Language spoken (root); place (state)	Sources
Tepary	mare'k	Yuma (Yuman); SW Arizona	[14]
	nókwina	Zuni (Penutian-Zuni); W New Mexico	[14]
	tepari	Opata (Uto-Aztecan); NE Sonora	[14]
	muní	Tarahumar (Uto-Aztecan); W Chihuahua	[14]
Scarlet runner	shaushana	Totonaco (Totonac); N Puebla	[150]
	ayocote	Nahuatl (Uto-Aztecan); N Puebla	[18]
	chomborote	Mam (Mayan); San Marcos	[17]
	piloy	Kakchiquel (Mayan); Chimaltenango	[17]
Year-bean	xuyumel	Totonaco (Totonac); N Puebla	[150]
	acaletl	Nahuatl (Uto-Aztecan); N Puebla	[18]
	dzich	Mam (Mayan); San Marcos	[17]
	piloya	Kakchiquel (Mayan); Chimaltenango	[17]
Lima bean	ib	Yucatec (Mayan); S Yucatán	[16]
	ixpanqué	Quiché (Mayan); Suchitepéquez	[149]
	pallar	Mochica (Paezan-Chimu); Lambayeque	Yacovleff and Herrera (1934)
	palatu	Cochabamba (Quechua); E Cochabamba	Cárdenas (1989)
Common bean	ju	Otomi (Oto-mangue); C Hidalgo	[16]
	etl	Nahuatl (Uto-Aztecan); C Mexico	[125]
	tatzin	Tarascan (Chibchan); NW Michoacán	[16]
	pi-zaa	Zapotec (Oto-mangue); C Oaxaca	[16]
	purutu	Quechua (Andean Amerind); C Peru	Soukup (1986)
	miculla	Aymara (Andean-Aymara); Puno-La Paz	Yacovleff and Herrera (1934)

[5]. Today as dry seed beans are the daily food of millions of people across Central America, Brazil, and eastern and southern Africa [6], and as snap bean a vegetable of worldwide importance [7]. But before Columbus landed in San Salvador of the Bahamas [8], beans were one of the few staples on which relied thousands of Amerindians for their daily food intake [9–12].

Being rightly acknowledged as "the meat of the poor" [13], these food plants of the legume family raise the following questions in their relationships with humans: which are these plants?, where and how did humans come into contact with them?, when did the relationships begin?, and why did they become established? Checking the naming of beans might be one way to start because names might tell us something about aspects of the relationships such as geographical origin, purpose, or history. Extended lists of vernacular names have been provided elsewhere for the tepary [14], the scarlet runner [15, 16], the year-bean [17, 18], the Lima bean [16, 19], and the common bean [16, 20, 21] (some of them reported in Table 14.1 as examples). Although such lists were not available to him, De Candolle [22] after studying the nature of names of food legumes available in the Old World, raised doubts about an origin of the later two beans in it. Going further along his argument, one notes the many derived words as the distance increases from the nuclear area of diversity where the bean crop seems present for centuries or millennia, and naturally the bean crop there has a specific name in the language locally spoken. One should note that all vernacular names in native languages in the Neotropics were given by the Amerindians of the first migration into the Americas after crossing Beringia some 20–15,000 years ago [23, 24]. If linguists agree on durations of 6000 years for the development of individual languages [25–28], this would mean that some of the vernacular names in the aforementioned lists and in Table 14.1 have been assigned to the respective bean crop almost since the beginning of the relationship with humans. The Oto-Manguean languages (e.g., Mixtec, Zapotec) trace back through glottochronology to 5200 years before present (b.P.) [20]; this author gave a date of 2400 years b.P. for the Zapotec term for bean, while the archaeological record for beans at Monte Alban gave 2000 years b.P. [29]. Interestingly, native languages in northeastern America before 700 years b.P. lack names for common bean [20], and this is compatible with a late introduction from Mesoamerica as shown by archaeological records [29].

Which Are These Plants?

Beans include five species that have entered the human *domus* [30], that is, have become domesticated or dependent on humans for survival through the harvest of pods, conservation and planting of seeds at the right time and place. This result has been obtained originally through the alteration of pod dehiscence [31] (Fig. 14.1);

Fig. 14.1 Pods of *Phaseolus vulgaris* L. (wild, *above*; and cultivated, *below*)

Table 14.2 Domestication events in *Phaseolus* beans

Bean species and vernacular name	Possible area(s) of last harvest	Sources
P. acutifolius A. Gray, tepary	NW of Neo-volcanic axis in Mexico	Garvin and Weeden (1994), Muñoz et al. (2006)
P. coccineus L., scarlet runner	Honduras	Spataro et al. (2011)
P. dumosus Macfady., year-bean	Volcanic mountains of SW Guatemala	[17]
P. lunatus L. (small-seeded), Sieva bean	W of Tehuantepec in Mexico	[75, 78, 157]
P. lunatus L. (large-seeded), Lima bean	SW of Ecuador and/or NW of Peru	[157], Debouck et al. (1987), [19]
P. vulgaris L. (small-seeded), common bean	W of Neo-volcanic axis in Mexico	[64, 79]
P. vulgaris L. (large-seeded), common bean	Central Peru: Apurimac and around it	[64]

conversely humans had the seed for their own consumption but were obliged to keep planting until now this induced artifact. The causative mutation responsible for the alteration of pod dehiscence is due to a major Quantitative Trait Locus in linkage group 2 where the QTLs controlling pod length and reduced dormancy are also found [32], and is likely ancient [33]. Authors [34–37] mentioned four domesticated species, but a fifth case has been established [17] because of the identification of a distinct wild ancestor with shattering fruits for all of them. The Neotropical genus *Phaseolus* of about 80 species [38, 39] has contributed seven bean crops (Table 14.2), all from the same clade [40]. Such a high number of cultigens is relatively uncommon in the plant kingdom; rather concentrated in few plant families [33], but has happened in other genera, namely *Capsicum*, *Cucurbita*, and *Solanum*, all in the Neotropics. One should note that the seven domestication events seem to be independent, in terms of botany, space, and time.

Although more data are needed for confirmation, the genus *Phaseolus* might be 7–10 million years old [40, 41]; it got split into two clades about five million years ago [40]. This happened during the Pliocene in the southwestern corner of Laurasia [42], while the closing of the Isthmus of Panama would be completed by 3.2 million years ago [43, 44]. About 4–3.5 million years ago, a separation happened that would result in the currently identified sections *Paniculati* (including the Lima bean) and *Phaseoli* (including the common bean, the scarlet runner, and the year-bean) [40, 41]. This would explain the genetic distance and impossibility to cross *P. vulgaris* with *P. lunatus* (reviewed by Debouck) [45]. About 2.5 million years ago [40], another splitting happened that resulted in the separation of the section *Acutifolii* (including the tepary) from the section *Phaseoli*, explaining the difficulty to cross the former with *P. vulgaris* [46, 47]. In the *Phaseoli*, the species would differentiate from one another about 2–1.3 million years ago [48, 49]. The major gene pools identified in wild *P. vulgaris* [50, 51] would have separated about 500,000 years ago [48], a duration over which minor morphological [52, 53], physiological [54], and genetic [55] differences become established. When the would-be Amerindians walked through Beringia into the Americas some 20–15,000 years ago [56, 57], they found some 80 wild species, two of them viz. *P. lunatus* and *P. vulgaris* being distributed north and south of Isthmus of Panama.

Where Did Amerindians Come in Contact with Beans?

The diversity of vernacular names given by Amerindians (Table 14.1, as an example) is a clear indication that these peoples knew many bean species for long in many parts of the respective ranges of distribution. So visual contact has been there for sure, but plant parts have been looked for too. Some use of wild *Phaseolus* species has been reported in the recent past: roots of *P. coccineus* [58] or *P. maculatus*, leaves of *P. angustissimus* [60], pods of *P. filiformis* [61], seeds of *P. acutifolius* [62] or *P. vulgaris* [63], and it is likely that such uses go well back into the past. But as aforementioned, in seven cases the relationships went further, five bean species became domesticated, with an enormous stock of varieties fully depending now on humans for survival.

Arguing about a place of domestication is uneasy for three reasons. First, it is not sure that the entire process extending over centuries can be completed in a small area. A good example in common bean is race “Nueva Granada” that originated in the central Andes [64] and acquired its final characteristics in the northern Andes [65]. Another example is cassava, where the domestication process could have started in southwestern Amazonia [66, 67], while this root crop was part of the classic Mayan agricultural system [68]. A third example is tomato with a domestication process initiated in the northwestern Andes and finalized in Mesoamerica [69]. A similar story is that of Flint corn, an early migrant to the northeast during the domestication of maize [70], but key for the development of hybrid corn when crossed with southern Dents [71, 72]. Second, it is not sure either that the geographic range of the wild progenitor has not experienced any change. Over short durations, for example a few centuries, oscillations in altitude are possible (in the Andes see Cardich) [73], but over millennia the wild bean progenitors have experienced major shifts in their ranges [48, 74, 75]. One could think about climatic alterations as the driving forces behind [76, 77], causing the highly structured gene pools in the wild, as evidenced by molecular marker studies [78–80]. However, it is possible to find and use markers that are neutral toward human selection, and with a low rate of mutation, mode of inheritance and such complexity so that a wild bean can be inferred as the progenitor of a cultigen. But the third call for caution may come from the gene flow between cultivated landraces and wild forms, and this has been shown to happen in Mesoamerica [81] and in the Andes [82]. So, local putative wild ancestors may reflect the genetic makeup of beans transported by people from elsewhere, if the molecular marker is not selected carefully. One reason behind this is that early domesticators rarely select directly for modifications in mating systems of crop plants, but on phenotypic traits visually attractive such as size or color of fruits or

Table 14.3 Founder effects associated with the domestication of the different bean species

Bean species	Sources
Tepary	Garvin and Weeden (1994), Muñoz et al. (2006), Schinkel and Gepts (1988), and Blair et al. (2012)
Year-bean	[17]
Lima bean	[78], Gutiérrez-Salgado et al. (1995), [19, 75, 157]
Common bean	Beebe et al. (2001), [83], Papa et al. (2005), Sonnante et al. (1994)

seeds. Bearing these remarks in mind, a few places have been identified (Table 14.2); as we see below let us call them "places of last harvest." They are certainly inconspicuous in relation to bean production today, and just look as isolated spots in the entire geographic range of the wild forms. A third domestication event in Lima bean, namely from wild forms distributed in Central America, cannot be discarded at this time [78]. We simply (!) need a better sampling of wild forms and landraces from that area as well as from tropical South America. The marked founder effect associated with bean domestications (Table 14.3) would suggest that the founding populations were indeed not numerous, leaving untouched most of the genetic diversity in the wild. We will see below why this low number is not surprising.

When Did the Relationships Initiate?

The relationships between beans as domesticates and humans started about 8000 years ago (for the common bean, on the basis of genetic data) [83]. Archaeological records tell us a different story particularly in Mesoamerica (Table 14.4), but one can anticipate that with further findings, genetic and archaeological data will eventually reconcile. Interestingly, the glottochronological data indicate a date of 3400 years b.P. for the Quiché in western Guatemala [20]. A parallel can here be drawn with maize, where recent archaeological findings [84, 85] in contrast with the old records [86, 87] have become much in line with genetic data [70, 88]. They all point to a single domestication in the Balsas region of Guerrero, Mexico, from the *parviglumis* teosinte about 8700 years ago [85]. This reconciliation for the beans pending, four considerations are however possible. First, particularly in Mesoamerica, five bean domestication events suggest that any of them could be equally ancient: early domesticators would hardly restart the process for another species if they have in hand an already well domesticated bean. But if not equally ancient, the domestication events look geographically independent (Table 14.2), perhaps along the same rationale. The hypothesis of relay domestication once discussed for common and tepary bean [89] is thus not certain, even if wild forms of both species can be found together at different sites [90]. Interestingly, the initial domestication events for the beans in Mesoamerica (Table 14.2) seem to be outside the Balsas region, although confirmation is pending for small-seeded Lima beans (MI group: Andueza-Noh et al.) [78].

Second, domestication events involving common and Lima beans are ancient in the Central Andes, with—for the time being—earlier dates as compared to W Mexico (Table 14.4). Again such events seem geographically independent (Table 14.2).

Table 14.4 Some archaeological records for different bean cultigens

Sites (place, state, country)	Years before present	Sources
For P. acutifolius		
Durango, Colorado, USA	1200	[95]
Tehuacan, Puebla, Mexico	2300	[29]
For P. coccineus		
Ocampo, Tamaulipas, Mexico	1100	[29, 128]
Río Zape, Durango, Mexico	1100	[29]
Tehuacan, Puebla, Mexico	500	[29]
Guilá Naquitz, Oaxaca, Mexico	1100	[29]
For P. lunatus		
Verde Valley, Arizona, USA	700	[95, 137]
Río Zape, Durango, Mexico	500	[29]
Tehuacan, Puebla, Mexico	1200	[95]
Dzibichaltún, Yucatán, Mexico	1200	[95]
Huacaloma, Cajamarca, Peru	2400	[29]
Guitarrero, Ancash, Peru	3400 (pC)	[29]
Ñanchoc, Lambayeque, Peru	8000 (pC)	Piperno and Dillehay (2008)
Chilca, Lima, Peru	5600 (pC)	[29, 97]
For P. vulgaris		
Tularosa, New Mexico, USA	2200	[88, 139]
Ocampo, Tamaulipas, Mexico	1300	[29]
Tehuacan, Puebla, Mexico	2300	[29]
San Andrés, Tabasco, Mexico	2300	Pope et al. (2001)
Huitzo, Oaxaca, Mexico	2100	[29]
Soconusco, Chiapas, Mexico	3000	Piperno and Pearsall (1998)
Darién, Valle, Colombia	2000	Kaplan and Smith (1985), Piperno and Pearsall (1998)
Chorrera, Manabi, Ecuador	2700	Piperno and Pearsall (1998)
Huacaloma, Cajamarca, Peru	2600	[29]
Guitarrero, Ancash, Peru	4300 (pC)	[29], Lynch et al. (1985)
Pichasca, Coquimbo, Chile	1400	[29]
Antofagasta, Catamarca, Argentina	5000 (pC)	Pearsall (1992), Rodríguez and Aschero (2007)

(pC): the beans were found in a preceramic horizon

The reader may wonder why only Lima and common bean were domesticated in South America. The reason is that only these two species crossed the Isthmus of Panama as wild forms, first the Lima bean [41] and later the common bean [48]. As explained elsewhere [17], *P. dumosus* (syn. *P. polyanthus*) exists in the northern Andes as a crop and as a weedy escape from cultivation. Because all maize races seem to come originally from Mexico and because Andean highland maize races seem to have a tropical origin [70], they migrated southeastward through Central American lowlands first! This would mean that there was a period of 2000 years when common and Lima beans were grown in the Central Andes in the absence of maize. Absence of maize could also have been the context of tepary domestication in

NW Mexico, but for ecological reasons (not sufficient rainfall to support the bean-corn association). As noted by Kaplan and Kaplan [91], this association came after the separate domestication of its components. But the abundance of beans in archaeological deposits seems to be linked to the presence of maize [29]. That said, it seems that archaeologists have focused their attention only on macrofossils, while microfossils (starch grains, mineralized hooked hairs) have not yet been exploited to the extent possible [92, 93]. And microfossils should be exploited at archaeological sites close to the putative sites of last harvest.

Third, in contrast with maize [87, 94], a transition in seed size from the wild state has not been found for any bean cultigen in archaeology so far [95, 96]. Many archaeological beans in size, shape, and even color [95, 97] appear fully modern. Because of the complex inheritance of seed size [98], one would thus expect earlier dates as compared to the few ones currently available. Fourth, although dating methods have altered some dates [29], archaeologists have often found early beans in the absence of ceramics (pC for pre-ceramic horizon in Table 14.4). The repetition of such absence across sites for the oldest records can hardly be considered as an artifact, even if ceramics already existed elsewhere. [The earliest records of pottery in the Americas are of 7000 years b.P. (Taperinha, Amazonia, Brazil) [99]; and 5300 years b.P. (Monsú, Bolivar, Colombia) [100]; with a couple of more recent independent inventions (coastal Ecuador: 5000 years b.P.; coastal Georgia: 4800 years b.P.) [101], but with no beans at these sites.] And this non-pottery context that some might think crucial for food processing [102] leads us to the reason(s) for bean domestication.

Why Have Beans Been Domesticated?

The answer to this question will always be speculative because the possibility of interviewing the first domesticators has gone some 8000 years ago as we have just seen. In addition, the only two scripts known in all pre-Columbian America—Mixtec and Mayan—appeared in the last millennium before our era [103, 104], quite late to record anything about the early domestication events, particularly in the Andes. Further, it is not certain that there would have been a single reason for the seven cases (Table 14.2), nor that the original reason would have remained the same during the first millennia of the domestication process, namely as food processing technology developed. In this regard, one has to remind that seeds of wild beans are likely to be toxic to humans because of the presence of, among others, prussic acid precursor [105], lectins [106], antitrypsin factors [107], α (alpha)-amylase inhibitor [108], and tannins [109]. The practice of soaking beans overnight and throwing the water away in the morning was not by chance, but a safe way to survive over a plate full of beans! The question thus might be tackled from different perspectives, such as: why beans at all? why *Phaseolus* beans and not species of another tropical legume such as *Mucuna*? why the beans for the purposes we know? why the populations at these locations (Table 14.2)? Bearing these points in mind, a couple of observations can be made successively about the need for dietary proteins, the avoidance of antinutritional factors, and the role of beans in incipient agricultural systems.

Fig. 14.2 Pods of *Phaseolus microcarpus* Mart. (*above*) and *P. chiapasanus* Piper (*below*)

First, the food value could well have been a driving force, if not directly at least indirectly (I mean the natural selection and survival of those who did succeed in domesticating beans). Domestication of beans in the Americas appeared in a non-livestock context, in contrast to pulses of the Old World (thus limiting our cross-comparisons). Absence of livestock may be the consequence of overhunting by the first Americans after crossing Beringia [110], or lack of appropriate behavior in the American fauna that survived such extinction [111]. During the first 10,000 years of hunting-gathering, the Amerindians had time to know the extent of flora across the Americas. It has been repeatedly demonstrated (e.g., the Mixe in Oaxaca [112] or the Tzotzil in Chiapas [113]) that Amerindians had a profound knowledge of their local flora within each territory. Because of the climatic alteration of "Younger Dryas" [114] and decreasing food resources [76], some Amerindians changed collective behavior and started planting and harvesting some plants out of that vast repertoire. Abundant grasses and legumes were likely candidates if it was to fill a carbohydrate-protein equation after all. A kind of "return on investment" may matter here: wild *P. microcarpus* Mart. (Fig. 14.2) and *P. vulgaris* (Fig. 14.1) might be equally widespread in some parts of central Mexico [38], but the tiny one-seeded pods of the former did not help toward domestication, that eventually affected the latter. The big pod of *P. chiapasanus* Piper [38] would surely confer a headstart (Fig. 14.2) but who knows it? Who has come across its few populations scattered in Chiapas, Oaxaca, or Veracruz [115]? Perhaps with the exception of *P. dumosus*, one can note that all wild bean progenitors have a wide range of distribution; endemic species such as *P. macrolepis* Piper, *P. oaxacanus* Rose, or *P. plagiocylix* Harms [38] were not domesticated. That characteristic of the range helped a priori making these legumes more familiar to would-be domesticators and helped *a posteriori* because planting—a fundamental act in domestication [30]—would be more successful with a wide range bean than with one of highly specialized ecology. In relation to the wide range, one should mention the hypothesis of the colonizing behavior of many of our crop wild relatives [35, 116–118], that is, the capacity to reproduce and expand quickly in human-made habitats. Notwithstanding the profound alteration of *Phaseolus* habitats over the last century, namely because of the expanding road network, it is likely to be the case for wild *P. coccineus*, *P. lunatus*, and *P. vulgaris*. According to Sousa-Sánchez & Delgado-Salinas [42], these three species have benefitted from human disturbance, but their expansion might also be the result of an intrinsic colonizing capacity. Back on the "return on investment" for would-be domesticators, pods of legume species such as *Desmodium*, *Macroptilium*, or *Mucuna*—although widely distributed in some parts of the Neotropics—would have had too many drawbacks (almost indehiscent loments, narrow width, itchy pubescence, respectively) to make them good candidates, while a few, widespread and relatively abundant *Phaseolus* species with high proteins and carbohydrates under low seed volume yet sizeable did. Paying further attention to pods—the first item caught by eye and hand, one notes that *Canavalia*, *Inga*, and *Phaseolus* with smooth pod epidermis in many widespread species contributed candidates for domestication.

Second, most legume species have defense mechanisms that protect their seeds, among them antinutritional factors to deter potential eaters, and *Phaseolus* species are no exception [107, 119, 120]. Although this point has already been discussed elsewhere [121], it might be worth updating. Eating young pods is an option, before antinutritional factors start accumulating in the seeds in the second fortnight close to maturity (for example, cyanide content in wild Lima bean: Frehner et al. [122]; or lectins in *P. lunatus*: Martin et al. [123]). In doing so, would-be domesticators are just following the example of birds (in spite of the differences in digestive tracks), as populations of wild beans show in pods damages by birds (Debouck et al.; also vouchers CR235450, US3168338 at these Herbaria) [124]. The use of green (immature to nearly mature) pod persists after ceramic was invented: the Mexicans today use the word "*ejote*" for it, an obvious modification of the word "*éxotl*" in nahuatl and in early codices [10, 125] for the same young pod. Given the very hard fruit cases of teosinte, Harlan [34] after his own testing proposed that the ancestor of maize was first used as a vegetable. Another use—chewing the sugary stalks —although still seen in Mexico [126] seems not confirmed in early domestication steps [93]. Of course cooking makes us essentially humans [102, 127] but as seen in Table 14.4, domesticated beans existed before the appearance of ceramics at these sites, although apparently at low frequency in the archaeological layers [128]. But grains might be put close to a heat source, and dry roasting has been shown to reduce haemagglutinating lectin and trypsin inhibitor activities in common bean [106]. Interestingly, when dealing with grains, Amerindians first thought about toasting, that is, the direct exposure of grains to a heat source. This reaction is particularly relevant in altitude sites above 2000 m.a.s.l., where longer durations are required to cook the beans given the lower atmospheric pressure [3]. Amerindians did that for maize: across Latin America, the most primitive races are popcorn (in Jalisco: "Reventador," [129], or "Nal-Tel," [130]; in México: "Palomero Toluqueño," [131]; in Cundinamarca: "Pira," [132]; in Junín: "Confite Morocho," [133]; in Cuzco:

Table 14.5 Some food systems often found in agricultural pre-Columbian Americas

Region	Main food sources	Complement	Sources
NW Mexico, Tarahumar	Maize, beans	Deer, mice	Lumholtz (1902)
Western Mexico	Maize, beans, agave, squash	Dog, turkey, deer	[130]
Central Mexico	Maize, beans, amaranth	Dog, fish, frog, turkey	Schwartz (1997), [12]
Costa Rica	Maize, beans, squashes	Tepesquintle	[34]
Colombia	Maize, potato, bean, manioc	Fish, game	Hernández de Alba (1963)
Coastal Peru	Maize, Lima bean	Fish, llama, dog	Schwartz (1997)
Central Andes	Potato, maize, bean, tarwi	Guinea pig, llama	[141]
Southern Andes	Maize, potato, bean		[11]
Araucania Chile	Mangu, potato, maize, beans	Fish, llama	Montaldo (1988), [145]
Guarani area	Cassava, maize, peanut, bean	Fish, rodents	Arenas (1992)

"Kculli," [133]; in Potosí: "Confite Puneño," [134]; in Cochabamba: "Checchi," [135]; in Jujuy: "Pisingallo," [136]). They did that for tepary and common bean in New Mexico [137], for common bean in Jalisco and Oaxaca of Mexico [138, 139], for tepary in Puebla of Mexico [95], or for common bean in the highlands of Peru and Bolivia [3, 80], and confirmed in pre-Columbian times in Peru and Chile [29], respectively. They did that for amaranth too [140, 141]. Some of these traditional uses of cooking without ceramics and the related germplasm have survived up to now, and are subject of renewed interest [3]. So, there were good reasons to pick up seeds of wild beans and to plant them for food, at least to avoid walking for hours or days to get back to the original population. And one day the non-dehiscent pod mutant appeared … There was no need to go back to the wild, no more worries about their ever shattering fruits, because a completely different evolutionary pathway was borne in a modified environment—the future cultivated field *milpa* or *chacra*. That mother wild population was the one of the last harvest! The early domesticators quickly shared their discovery through incipient seed systems which favored genetic isolation from the wild and the return of their feared dominant genes.

Third, as aforementioned, bean became abundant in the (Mesoamerican) record once maize agriculture intensified. As apparent in Table 14.5, maize (or Indian corn, a widely accepted vernacular name among English-speaking immigrants into the New World) turned into the cornerstone of pre-Columbian agriculture, in Mesoamerica where it was domesticated and in South America where it was introduced [70]. The protein of maize was deficient in two essential amino acids, lysine and tryptophan [13]; the former was complemented by beans, and the latter by some animal protein (and partly the potato in the Andes). That type of diet was unconsciously selected because it made people well fed [142] and secured the physical and intellectual development of childhood. McNeill [143] noted that domesticated animals played a marginal role in human food habits in pre-Columbian America. With no buffering that represents livestock in agricultural systems, many Amerindians were year after year pending on the success of their maize and bean crops. The beans being more tolerant to drought in drought-prone area such as Mesoamerica, Amerindians always looked after them. Having not found any grass alternative to Indian corn in terms of productivity per plant, they never gave up their maize varieties. Such lack of alternative and the genetic plasticity of maize can perhaps explain much of its diffusion from western Mexico northward up to Canada [13, 144] and southward down to Chile [145], almost matching that of beans [146, 147]. At least for the five bean cultigens (just as it was for maize), the domestication process seems continuous, not abandoned, even though tepary could have suffered a (recent) regression because of the watering facilities provided in Aridoamerica since the 1900s [14]. Market forces since the 1950s—linked to urbanization?—have not helped either to integrating the other three cultigens [148]. But beyond nutritional aspects, the maize-bean association seems to have been a performant agronomic system, namely thanks to the addition of squash, in order to limit soil erosion [147]. Again the acute sense of observation of Amerindians might have helped here because there are spots in Mesoamerica where wild beans climb on teosinte stalks (in Huehuetenango: McBryde [149]; in México: Delgado-Salinas et al. [150]; in Michoacán: Miranda-Colín [151]). Interestingly, this system was widely adopted with original and mutual selections of the three crops much beyond their original places of domestication, often against a latitude and photoperiod [152] and altitudinal gradient. And one should note that apart from the brilliant idea to domesticate individually beans, maize, or squash where unconscious elements might have played a role, the other brilliant idea—and fully conscious—was to combine the three crops together into a relatively stable agricultural system. Metallurgy came late (approxim. 3000 years b.P., for limited bronze axes) in pre-Columbian history [153], and thus agricultural implements were limited. Interestingly, the illustrations by Guamán Poma [154] showed the Incas using the *chakitaqlla* or foot plough, not a plow driven by a llama, although the animal was there for limited carrying of goods. So, externalities such as lack of draught animals and the sole availability of manpowered tools (the *macana* or planting stick!) pushed Amerindians' skills in plant breeding to the limits as well noted by Jack Harlan [30]; their resourcefulness, acute sense of observation, and selections came along with unique and superb results because their crops responded. This was a brilliant anticipation of what plant breeding can achieve.

Concluding Remarks

We had to explain why beans at all were domesticated, and we realized that the Amerindians did the right pick among hundreds of options left in the Neotropical flora for their dietary protein intake. With game becoming rare and uncertain, we can understand their switching long hours of walk for planting a few wilds close to their settlements. This change in collective (because it goes beyond a single individual) behavior led to a strategy of reducing risks because the planted stand of wild beans was a relatively secure source of food, till the non-shattering pod mutant appeared. Table 14.2 presents places of last harvest because the non-shattering pod mutant had more chances to be picked up in an artificial stand than a natural one. On purpose we are no longer indicating a domestication site for the bean cultigens because these artificial stands might be distant from the populations of last harvest. The low probability of the mutation itself and of its being noted and picked up (double low frequencies, the second one linked to human behavior being impossible to calculate!) explains the few domestication events, in common bean 2–3 [50, 64, 155, 156] in a range of wild populations extending over 8000 km from Chihuahua down to San Luís [121]. With an even wider range [38], the tropical wild form of Lima bean was affected by 1–2 domestication events [78, 157]. It is perhaps the need for food in contrasting environments that explains why five bean cultigens instead of one have been domesticated, with one per environment. And the places reported in Table 14.2 are not those where two wild ancestors have been found together [45]. A similar scenario of double low probability would explain the single domestication event in the other three bean cultigens.

The relationships between beans and humans have been long and fruitful because they allow both species to expand. For the first 5000 (or more) years, that expansion took place in the Americas, allowing together with maize an improved diet, a sustainable agricultural system, and there onward a sustained demographic growth and a social stratification. Have you seen the most prestigious pre-Columbian civilizations (of Mesoamerica) on another food basis than the corn-beans association? In this system, beans brought sustainability from a nutritional perspective for humans and for the soil (nitrogen input and reduction of erosion). Over the last 500 years, a similar expansion took place in the Old World with similar benefits, particularly in Africa [158]. Understanding these relationships in the Americas above all during the early steps of bean domestication can have a very significant impact in the new territories of bean adoption, namely the Old World tropics and subtropics, where foreign crops (mostly American: maize, beans, peanut, cassava, sweet potato) have been and continue to be critical to food security. Under similar ecological conditions it is well known that crops perform better outside their centers of original diversity [159], being free from their everlasting co-evolving pests. And farmers worldwide have been among the first to note this, thus the speed of adoption; for example, the “patani” (*P. lunatus*) [160] of the Philippines could have landed there together with the “chilli” (*Capsicum annuum* L.) [161] with the galleons sailing from Acapulco to Manila as early as 1570 a.D. [162].

Beyond expansion, another question that can be asked is whether or not we as modern humans have been equal to the domestication efforts by Amerindians and the bean biological heritage they left us. The use of race “Mesoamerica” of common bean [65] has been wide [163], less so the other races. And bean breeders have not always realized that there are four more bean crops to breed in addition to common bean. Obviously, bean breeding nowadays will be in reply to demand; so is our society sufficiently aware of coming food challenges and of options provided by *Phaseolus* beans? We may finally put hunger out of the list of Millennium Challenges, to quickly turn into overnutrition and health problems because of excessive consumption of animal proteins at the expense of plant proteins [164]. In view of the increase of type II diabetes in many countries [152], returning to more traditional diets based on food legumes is perhaps a cheap way to keep people healthy. Facing an emerging energy crisis in food production, transportation, and processing [165], where the energy cost of animal proteins needs to be reassessed, green shelled beans may be an option to recover. Equally, the popping beans that we know were present in Mesoamerica might turn into an example of a lost opportunity. As never before, understanding the early steps of crop domestication in the Neotropics through multidisciplinary research has been so relevant.

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Chapter 15

Homo sapiens–Cucurbita interaction in Mesoamerica: Domestication, Dissemination, and Diversification

Rafael Lira, Luis Eguiarte, Salvador Montes, Daniel Zizumbo-Villarreal, Patricia Colunga-GarcíaMarín, and Mauricio Quesada

Abstract *Cucurbita* are monoecious and creeping plants including 20 taxa and 15 species. In Mesoamerica, four species were domesticated or diversified after domestication in other geographic areas: *C. argyrosperma C. pepo*, *C. moschata*, and *C. ficifolia*. The earliest evidences of the domestication of *Cucurbita* date 9000 BP from Southwestern Mesoamerica and 10,000 BP from Southwestern Ecuador. The main targets of human selection were the seeds contained in larger and less bitter and toxic fruits (due to cucurbitacins), without vine detachment. *C. argyrosperma* ssp. *sororia* from México to Central America warm-humid and subhumid climates is considered the wild ancestor of the domesticated *C. argyrosperma* ssp. *argyrosperma*. For *C. pepo*, the proposed ancestor of the domesticated populations of

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México is *C. pepo* ssp. *fraterna* from northeastern Mexico, while the putative progenitor of the cultivars from in North America is *C. pepo* ssp. *texana* from eastern United States. For *C moschata*, there are two hypotheses as to its domestication region: southern Mesoamerica, or from the lowlands of Colombia and southern Ecuador. Cultivated *C. ficifolia* is found from the Mexican highlands south to Chile and Argentina, its center of domestication is either Central America or southern Mexico/Central America, as supported by linguistic evidence, or the Andes, as indicated by archaeological evidences from Peru dated at 3000 BC. Humans spread cultivated *Cucurbita* inside and out of Mesoamerica, structuring a complex agricultural system along with corn (*Zea mays*), and different species of beans (*Phaseolus* spp.) called "milpa," that were established in a wide range of environments.

Keywords Genetic resources • Domestication • Pumpkin • Squash • Mesoamerica

The genus *Cucurbita* is a well-known domesticated species which, in Spanish speaking countries are commonly referred to as "calabazas," "zapallos" or by several indigenous terms, while in English speaking countries they are known as "squashes," "pumpkins," "zucchinis," or "gourds" [1–3]. Mature and ilmmature fruits, as well as seeds of domesticated species of this genus have been a very important element in the diet of large segments of the world's population. In many Latin American countries, the flowers and some vegetative parts (e.g., tender young tips of stems or "guías") are also eaten as vegetables [1, 4, 5]. Wild species have become an important source of adaptive genes related to resistance to crop-harming pathogens. *Cucurbita* plants are monoecious and creeping plants; flowers are gamopetalous, with tubular-campanulate corollas and very showy, yellow, bright yellow, or pale orange petals; staminate or male flowers have column shaped stamens, with more or less coherent filaments, and the anthers are joined into a cylindrical or tight pyramidal structure; pistillate or female flowers have an inferior ovary with numerous horizontally placed ovules; styles are semi-free at the apex or fused along their entire length; stigmas are large, fleshy, or more or less sunken or lobulate, and slight modifications can be seen in the structure of the perianth with regard to the staminate flowers; fruits are pepo type, balloon, ovoid, or rarely pyriform shaped, the surface is generally smooth, with no ornaments, white, yellow, or green colored, with or without spots and/or fringes; seeds are oval, oval-elliptic, or oval-lanceolate, compressed or more or less tumescent or inflated, with a smooth center or rarely pitted or scarified, white, cream colored, blue-gray-green or black, with or without differentiated margins which can have the same or a different color and/or texture as the seed's center [5]. Flowers of *Cucurbita* species open very early in the morning and are pollinated by solitary bees of the genera *Peponapis* and *Xenoglossa* [6].

According to the most recent phylogenetic and systematic studies of the family, *Cucurbita* belongs to the Cucurbiteae tribe, Cucurbitoideae subfamily,

Table 15.1 The 20 taxa of *Cucurbita*

1. ***C. argyrosperma*** **Huber ssp.** ***argyrospermaa***	Argyrosperma Group
2. *C. argyrosperma* ssp. *sororia* (L.H. Bailey) Merrick & Bates[a]	
3. ***C. pepo*** **L. ssp.** ***pepo***[a]	Pepo Group
4. C. pepo ssp. *fraterna* (L.H. Bailey) Andres[a]	
5. C. pepo ssp. *texana* (Scheele) I.A. Filov	
6. ***C. maxima*** **Duch. ex Lam. ssp.** ***maxima***	Maxima Group
7. *C. maxima* ssp. *andreana* (Naudin) I.A. Filov	
8. *C. ecuadorensis* Cutler & Whitaker (suggested by Sanjur et al. 2003)	
9. *C. okeechobeensis* (J.K. Small) ssp. *okeechobeensis*	Okeechobeensis Group
10. *C. okeechobeensis* ssp. *martinezii* (L.H. Bailey) Walters & Decker-Walters[a]	
11. *C. digitata* A. Gray[a,b]	Digitata Group
12. *C. cordata* S. Watson[a,b]	
13. *C. palmata* S. Watson[a,b]	
14. *C. foetidissima* H.B. K.[a,b]	Foetidissima Group
15. *C. pedatifolia* L.H. Bailey[a,b]	
16. *C. scabridifolia* L.H. Bailey[a,b]	
17. *C. radicans* Naudin[a,b]	
18. *C. lundelliana* L.H. Bailey[b]	Species not placed in any group
19. ***C. ficifolia*** **Bouché**[b]	
20. ***C. moschata*** (**Duch. ex Lam.**) **Duch. ex Poir.**[b]	

Bold face names domesticated taxa

[a] Perennial taxa

[b] Taxa represented in Mexico

together with the genera *Sicana*, *Peponopsis*, *Polyclathra*, *Schizocarpum*, *Calycophysum*, *Tecunumania*, *Anacaona*, *Penelopeia*, *Abobra*, *Selysia*, *Cionosicyos*, and *Cayaponia* [7–9].

Although for many years *Cucurbita* was thought to have between 20 and 27 species (e.g., 10–12), according to Lira et al. [5] this genus includes 20 taxa belonging to 15 species (or groups of species), which, due to the ecology of their habitats and the length of their life cycle, have traditionally been divided in two large groups: xerophytic species, with tuberous perennial conservation roots, and species from more or less mesophytic environments, annual perennials or short-lived, but with fibrous roots (Table 15.1). In Mesoamerica, four species of the mesophytic group became domesticated or diversified after domestication in other geographic-cultural areas: *Cucurbita argyrosperma* Huber, *C. pepo* L., C. *moschata* (Duch. ex Lam.) Duch. Ex Poir., and *C. ficifolia* Bouché. A sample of the Mexican diversity of these species is shown in Fig. 15.1.

Fig. 15.1 Fruits diversity of some wild and the four domesticated taxa of *Cucurbita* in Mexico. (**1**) *C. argyrosperma* ssp. *sororia*; (**2**) *C. argyrosperma* ssp. *argyrosperma*; (**3**) *C. ficifolia*; (**4**) *C. moschata*; (**5**) *C. pepo* ssp. *fraterna*; (**6**) *C. pepo* ssp. *pepo*; (**7**) *C. lundelliana*; (**8**) *C. okeechobeensis* ssp. *martinezii*

Homo Sapiens–Cucurbita Interactions in America

Homo–Cucurbita interactions began when hunting-gatherer groups arrived in America's southwestern and central plains c. 12,000–11,000 BC. Survival and dispersion of humans across the new continent depended on fire, essential to defend themselves from predators, to keep warm and prepare food, and to guide, lure, and surround animals when hunting to establish annual grass communities and to produce more food [13]. Culture was based on gathering, grinding, and eating grains and seeds which are important food sources of carbohydrates, lipids, and proteins. Grinding was done with modified rocks. Starch-rich tubers, stems, roots, grains, and seeds were cooked in wood stoves and buried ovens, archaeological remains of which have been found in Europe and Asia before 32,000 BC, as well as in paleo-Indian sites in North America's central plains (10,500–10,000 BP [14, 15].

During the initial transitional stage between gathering and agriculture, fire was a sort of pre-human selection that favored pre-adapted plants and later domesticated in the New World [13]. Paleo archaeological evidences from 10,000 to 7000 BP suggest that Mesoamerica's agricultural system was based on clearing the land of vegetation using the "slash and burn" system, and archaeological records indicate that food transformation was based on the use of stones modified for the purpose of grinding grains and seeds, fires, and underground ovens [16–19].

The first archaeobotanical evidences of the domestication of *Cucurbita* date from the Pleistocene's last period in Southwestern Mesoamerica (9000 BP) and Southwestern Ecuador (10,000 BP) [19–21].

The vegetation in these areas corresponds to tropical dry forests, with warm semi-humid climate. The archaeological remains indicate that humans selected, harvested and ground seeds, and point to two early simultaneous processes, independent from the domestication of *Cucurbita* in America where the target of human selection, and source of lipids and proteins, were the seeds contained in fruits [19], nutritional elements that complemented the carbohydrates from corn and beans in Mesoamerica [22].

Seeds were collected for their high nutritional value and tastiness once the toxic substances were rinsed out [23]. The key morphophysiological characteristics of *Cucurbita* that seem to have favored domestication could be their pre-adaptation to human disturbances (clearing forests through slash/burn), and the very notorious fruits, available during the entire dry season and/or winter [1]. Because seeds of *Cucurbita* species were recurrently selected from large and less bitter fruits, without detachment from the vine, their dispersal mechanism as well as their ability to adapt to their natural environment could have been modified, making it necessary to manage them through agriculture in order for them to survive and produce subsequent generations.

For *Cucurbita*, the interaction with humans meant: (a) decrease in the fruit's ability to detach from the peduncle possibly due to a weakening of the pericarp's rigidity and the widening of the peduncle at the base; (b) decrease in physical defenses with the change of size and shape of the phytoliths and silicified hairs in leaves, stems, and fruits; (c) decrease in chemical defenses with the decrease or elimination of bitter and toxic substances (e.g., cucurbitacins) in the fruit; (d) decrease in adaptation capacity to random rainfall from the increase in homogeneity and germination speed; (e) change in resource assignment through the increase in fruit and seed size and, simultaneously, with decrease in the number of fruits per plant and seeds per fruit; (g) change in growth habit, from indeterminate creeping to determinate semi-arborescent or rosette.

For *Homo*, the interaction meant: (a) food security by the decreased rate in detachment of the mature fruit from the vine; (b) more and better food quality to satisfy the nutritional requirements; (c) complementing the carbohydrates from corn and proteins from beans; (d) increase in energy expenditure used to modify the environment (agriculture) while trying to achieve plant survival. The importance of *Cucurbita* in ensuring the survival and adaptation to the new Mesoamerican environment of Homo is culturally reflected in the language of Proto Otomangue groups dating to before 7040 BP [24].

Domestic *Cucurbita* was mainly dispersed by *Homo sapiens* early on from Mesoamerica to South America and vice versa, as shown by evidence of its presence as part of Panama's southern slope archaic diet since before 7000 BP [25–27]. Macro- and micro-archaeobotanical and genetic-molecular evidences have been key to understanding Homo sapiens—Cucurbita historical interaction. Macro evidences of selective human pressure have been registered through changes in seed size, thinness of the testa, shape and size of the base of the peduncle in the insertion point to the fruit, and thickness and rigidity of the pericarp [28, 29].

Micro-archaeological evidences include morphological and size changes of the phytoliths, silicified hairs in fruits, stems, and leaves, and size, shape, and color of the starch grains [30]. The genetic and molecular evidences are the molecular variation in the mitochondrial intron 2 *nad1* [31], and the polymorphism in several genes which controls important phenotypical attributes such as rigidity of the fruit's pericarp, shape, and amount of phytoliths, as well as the production of chemical substances related to the bitterness of the fruit's pulp [32].

Domestication and Diversification of *Cucurbita argyrosperma* in Mesoamerica

Reproductive compatibility and genetic and molecular morphological evidences suggest that the *Cucurbita argyrosperma* ssp. *sororia* is the wild ancestor of the domesticated group *Cucurbita argyrosperma* ssp. *argyrosperma* [1, 4, 5]. The subspecies *sororia* is distributed from México to Central America, in regions with warm-humid and subhumid climates, in Tropical Dry Forests, as well as the transitional areas between pine-oak forests; its altitudinal distribution ranges from sea level to 1800–1900 m.a.s.l. Subspecies *sororia* show morphological and physiological traits of pioneer plants: heliophyle, germination promoted by fire, creeping and climbing growing habit, occupying open spaces in the vegetation such as sand limo banks next to rivers and streams. The morphological characteristics of the fruit in populations of this subspecies suggest dispersion through physical means: flotation and down-slope rolling after detachment from the peduncle, and possibly dispersion by animals who feed from the fruits. These plants have a large amount of stiff and silicified hairs on the leaves, stems, and immature fruits, as well as high contents of cucurbitacins as defense mechanisms against predation and produce high numbers of small fruits per plant and a high number of small seeds per fruit [4, 5]. Genetic, molecular, biogeographic, and archaeobotanical evidences suggest that humans domesticated the populations from Tropical Dry Forest of the Balsas-Jalisco biogeographical region approximately 9000 BP years ago [19, 21, 31].

Ethnobotanical evidences indicate that, since the archaic period, seeds of this subspecies, together with grains and seeds of *Zea mays* ssp. *parviglumis*, *Phaseolus vulgaris* var. *Mesoamericanus* and *P. lunatus* var. *silvester*, have been an important part of the diet of human groups settled in this region [22]. Other archaeological records suggest an early diversification, posterior to the initial domestication before 7000 BP, in the SW region of the United States and NE of México (var. *callicarpa*), in Tamaulipas (var. *argyrosperma*) and in the Valley of Tehuacán (var. *stenosperma*) [4]. The selection of large and less bitter fruits with large seeds and thin skin, which remain in the vine, could have been the driver of human selection to the domestication of this species, and conducted it to depend on *Homo* through a diminished dispersion capacity and less defense against predators.

Domestication and Diversification of *Cucurbita pepo* in Mesoamerica

Morphometric and molecular studies, as well as studies on artificial and spontaneous hybridization, suggest two independent domestication events for *Cucurbita pepo*. Thus, while the ancestor of the domesticated populations distributed in México is *C. pepo* ssp. *fraterna* from northeastern Mexico, *C. pepo* ssp. *texana* from eastern United States would be the putative progenitor of the cultivated types in North America [5, 31, 33–37]. Populations of *C. fraterna* have only been reported for some localities in the states of Tamaulipas and Nuevo León (not recently found in that locality), while populations of *C. texana* have been reported for Texas, Louisiana, Arkansas, Mississippi, Alabama, Missouri, and southern Illinois; both taxa grow in low altitudes, and are climbers or creepers in open and fertile places such as sandy riversides and altered sites; their fruits are small, extremely bitter due to the presence of cucurbitacins, fall easily from the vines, and they float and are transported by water dispersing the seeds to inundated lands [5, 33–35].

On the other hand, the oldest archaeological records in México of the domesticated *C. pepo* correspond to the Valley of Oaxaca (10,000 BP), Tehuacán (7900 BP), and the Ocampo caves in Tamaulipas (6300 BP), while the oldest records in the United States date to 5000 and 3800 BP [28, 29, 38]. The domestication traits in the edible *C. pepo* ssp. *pepo* are similar to the desirable traits selected by humans to domesticate *C. argyrosperma* ssp. *argyrosperma*, including selection for lipids and proteins, larger and less bitter fruits and seeds, and seeds with a thin testa.

Ethnobotanical records and other evidences suggest that many edible and ornamental commercial cultivars have been produced all over the world and that numerous local varieties of *C. pepo* are cultivated in America [2, 3, 5]. Thus, for example, in Mesoamerica there are native varieties (known as “tsol” in the Yucatan Peninsula and Guatemala) that grow near the sea level, in semidry climates, and over limestone soil, while other (named “güiches” in the state of Oaxaca and “güicoy” in Guatemala) are cultivated above 1800 m, with colder climates and sometimes over highly eroded soils [5]. This huge genetic variation indicates adaptation capabilities of this species to different environments achieved through selection and human management. This genetic diversity, however, does not represent an important source of genes resistant to pests and diseases, since *C. pepo* group is probably the group of species of *Cucurbita* with the greatest susceptibility to the most important viral diseases [39, 40]; additionally, species that might represent a secondary gene pool are scarce, since most of the attempts to hybridization *C. pepo* taxa with other wild or cultivated species have required special techniques such as embryo culture [39].

Introduction and Diversification of *Cucurbita moschata* in Mesoamerica

Cucurbita moschata was initially considered an Old World crop, but now is clear that it was domesticated in America [41], although its center of origin remains unknown. There are two hypotheses as to its domestication region: southern Mesoamerica [3], and the other one from the lowlands of Colombia and southern Ecuador [20, 30]. Archaeobotanical records from human settlements in Las Vegas, southern Ecuador (10,130 and 9320 BP), revealed the presence of size and shape sequences of phytollites from *C. ecuadorensis* and *C. moschata*, pointing to the selection, cultivation and early domestication of pumpkins [20] and, possibly to *C. moschata* was domesticated from *C. ecuadorensis* in lowland places of tropical dry habitats. Archaeological remains consisting of phytollites of *C. moschata* from soil deposits from several human refuge sites in Panama in tropical dry habitats indicate that this crop had spread to Panama before 8600 BP [25], while the oldest Mexican archaeological records of this species from the Ocampo caves (Tamaulipas, NE Mexico) dated in more than 5000 BP, which also suggest its early presence in Mesoamerica (see several references in [5]). On the other hand, an important morphological diversity of local races has been described for *C. moschata* in southern Ecuador to northern Colombia [42] suggesting this area as the center of origin of this crop.

Although these data suggest a South American origin for *Cucurbita moschata*, different sources of evidence show that this species is very closely related to *C. argyrosperma* and far from *C. ecuadorensis*, which is closer to *C. maxima* [1, 4, 31]. Furthermore, *C. ecuadorensis* thrives in disturbed environments with semi-humid and humid climates in southern Ecuador, from 0 to 400 m.a.s.l. [5, 43], while *C. moschata* grows mainly in warmer climates and higher humidity, from 0 to 2300 m.a.s.l., [1, 5, 12]. Furthermore, recently a closer genetic relationship between *C. pepo* and *C. ecuadorensis* than between *C. moschata* and C. ecuadorensis has been proposed [44].

In summary, it is clear that the wild ancestor of *C. moschata* is still unknown, and northern Colombia seems to be the most promising area to discover it [1]. Ethnobotanical and botanical evidences indicate that in this area can be found cultivars with high diversity of fruit types, as well as cultivated plants occasionally with bitter fruits, suggesting hybridization with a local and still unknown wild *Cucurbita* species [1].

Regardless of the center of origin of *C. moschata*, its early introduction to Mesoamerica meant diversification through selection, agricultural management, and diversity of agro-ecosystems and culinary systems to which it was incorporated, resulting in an expansion of its distribution area and the adaptation to multiple environments. Accordingly, the genetic resources of this species are very rich considering the wide distribution of its traditional races and varieties, and the numerous cultivated commercial varieties produced in the United States and other world regions. Unfortunately, this genetic diversity has only been partially studied with molecular markers. Thus, relatively high genetic diversity values have been found in Mexican accessions of *C. moschata* (37 % of polymorphic loci) compared to other *Cucurbita* species also cultivated in the country [45].

On the other hand, important information exists, for example, for the germplasm collections of this species mainly from Mexico and Central America and housed at CATIE in Costa Rica, which were analyzed using PCR SSCP and chloroplast sequence data [46]. The results of this study show that Mexico had the highest values of total heterozygosity and genetic diversity, while Panama showed the lowest values. According to all this information, Mexico should not be discarded as an area of great interest for the future study of the genetic diversity of this species.

Cucurbita ficifolia in Mesoamerica

Cucurbita ficifolia has been subject to less scientific study than other domesticated species of Cucurbita. Nevertheless, several important facts have been clarified by Thomas Andres [47], and can be summarized as follows:

1. *Cucurbita ficifolia* is an annual and American plant, which is generally cultivated in areas with cool climate from 1000 to 2800 m.a.s.l. This altitudinal restriction is a characteristic distinguishing it from other cultivated species of the genus which, in general, can grow in a wider range of ecological conditions.
2. It is by far the least variable species of the cultivated *Cucurbita*, since morphologically the most important variation is in dimensions and color patterns of the fruits (white to green fruits with color patterns as spots or white stripes), and seeds (white, tan to dark brown or black). Low variation of this species was also found in isozymes studies.
3. Its Latin American distribution ranges from the Mexican highlands south to Chile and Argentina and is also cultivated in many tropical highland regions of the world.
4. The precise location of its center of domestication is still uncertain. Thus, some authors have proposed that its center of origin is Central America or southern Mexico/Central America (supported by linguistic evidence as the wide use of names based on the Nahuatl name “chilacayohtli” as far south as Argentina), and others suggest that its center of domestication is located in the Andes (supported by archaeological evidences as seeds and fruit peduncles from Peru dated at 3000 BC). These two hypotheses, however, are not conclusive because of the strong reproductive incompatibility between *C. ficifolia* and the wild taxa of the genus.

5. All these data suggest that the wild relative or ancestor of *C. ficifolia* could be a species not yet described (or maybe extinct) from South America.

More recently, studies of a sequence of an intron region from the mitochondrial gene nad1, and chloroplast restriction fragment length polymorphism (RFLP), have suggested that *C. ficifolia* is basal to all other mesophytic *Cucurbita* species [31, 35], whereas other with RAPDs have corroborated that this species has the lowest genetic diversity of the four species of *Cucurbita* cultivated in Mexico [45]. Further ethnobotanical and systematic studies are needed in order to have a better and more comprehensive knowledge of this species, especially in South America where it seems more feasible to find its ancestor, as well as more genetic variation.

Discussion

How did the new phenotypic characteristics of *Cucurbita*, product of mutations or reorganizations of a human-selected genome become fixed in conditions of intense genetic flux between wild and selected plants? The recurrent positive selection by *Homo* of individuals with the desired traits phenotype, and the continuous elimination of individuals with undesired wild characteristics, must have been an important—but not the only—evolutionary force. Reproductive isolation through mutant selection with a short life span (reproductive isolation), and cultivation outside the distribution of wild individuals (geographic isolation) played a very important role [13]. Besides the new mutations, the effects of the genetic expression and the influence of environmental conditions caused by cultivation on the new phenotypes, originated genetic pools with a high phenotypic diversity which humans gathered, selected, and disseminated for a long period of time. It is well known (although not yet evaluated in *Cucurbita*) that gene expression during plant development (plasticity) enable different phenotypic paths in adult plants and that the new phenotypes acquire the potential ability to fix themselves if the new ecological conditions remained unchanged by the crop during multiple generations [48].

Archaeobotanical records suggest that humans spread domestic populations inside and out of Mesoamerica, structuring a complex and nutritionally complementary agricultural system during the early archaic era with corn (*Zea mays* L.), beans (*Phaseolus* spp.), and pumpkins (*Cucurbita* spp.) called “Milpa” [22]. Milpas could be established in multitude of environments. The wide phenotypical plasticity of corn enabled it to adapt along a wide environmental range where it humans groups settled, and although no species of *Cucurbita* showed this plasticity, their differential or variable adaptation range enabled structuring the milpa system in different thermal levels within its ecological range which, in general terms, goes from 0 to 3000 m.a.s.l.

It is important to highlight that the genetic diversity of *Cucurbita* in Mexico could be in risk due to the potential genetic exchange between the landraces and wild relatives of the domesticated species, and genetically modified organisms. It has been documented, for example, spontaneous genetic exchange between *C. argyrosperma* ssp. *argyrosperma* and *C. pepo* ssp. *fraterna* in Tamaulipas [49] and between *C. argyrosperma* ssp. *argyrosperma* and *C. argyrosperma* ssp. *sororia* in Jalisco [50]. On the other hand, recent studies in domesticated and wild plants of *Cucurbita pepo*, suggest that the F1 generation does not represent a strong barrier to the introgression of neutral or "beneficial crop genes" into wild populations of this species [51]. Additionally, experimental studies showed that plants genetically modified of *Cucurbita pepo* ssp. pepo with genes that confer resistance against virus infection can produce fertile hybrids with the wild *C. argyrosperma* ssp. *sororia* across F1, F2, and backcrosses, showing that the transgene follows Mendelian inheritance in certain plant families as the proportion of virus-resistant transgene pollen increases in experimental crosses across generations [52]. In response to this potential threat, the authors of this chapter are participating in a project, within whose objective is to determine the effect of transgenic introgression into several Mexican wild taxa of the genus *Cucurbita*.

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Chapter 16
Genetics and Ecology of Wild and Cultivated Maize: Domestication and Introgression

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Abstract Maize (*Zea mays* subspecies *mays*) has been culturally and economically a very important crop since it was domesticated from its wild relatives, the teosintes (both the lowlands teosinte, *Zea mays* subspecies *parviglumis* and the highlands teosisnte, *Zea mays* subspecies *mexicana*) in Mexico. In this chapter, we review molecular studies analyzing different aspects of the genetic resources, domestication, phylogeography, and other aspects of the evolution of maize and teosintes, including niche modeling. The genetic studies range from isoenzymes to single nucleotide polymorphisms and other genomic and transcriptomic studies. Both cultivated maize and wild teosintes have high levels of genetic variation and signals of strong local adaptation. Currently, the most accepted hypothesis on maize origin indicates that domestication occurred 9000 years ago in a single event in southern Mexico from the lowland subspecies, *Z. m. parviglumis*. According to these ideas, later maize spread into higher elevations through adaptive introgression with highland teosintes, *Z. m. mexicana*. But these ideas are still open to discussion, as better data are needed. Since the origin of maize, there has been strong ongoing artificial selection that has allowed maize to diversify and spread globally and to highly new environments. This intensive selection in maize has left strong molecular signals of selection on a variety of genes that go from domesticated genes to improvement genes. To help respond to climate and global changes, it will be important to determine genes of agronomic importance for tolerance (weather, plagues) and improvement (increase in productivity) to cope with these changes.

Keywords Genetic resources • Domestication • Phylogeography • Maize • Mesoamerica

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Introduction

Maize, *Zea mays* subspecies *mays*, was the central crop species of Mesoamerican pre-Hispanic cultures, and it is still a fundamental part of Mexican and Central American cultures. Maize is also an important crop for human and cattle consumption in many countries (see [1] for a recent review about uses in maize). In addition, the wild relatives are also used in different regions of Mexico, for instance, for cattle consumption during the dry season, when other plants are scarce [2]. Since its domestication from teosinte, different maize races and varieties have been developed for different uses and growth conditions [1, 3], resulting in an impressive range of morphological, physiological, and genetic variation. There have been important, traditional genetics, genomic and genetic engineering developments in maize, all of them having the potential for further improving this crop production. We consider it relevant to understand the interactions that humans have had with maize, which have allowed their continuous improvement since its domestication, ca. 11,000–9000 years ago.

Zea mays is a monoecious monocotyledon annual grass; it is wind pollinated and it is widely planted in Mexico and several other countries, being adapted to grow in different soil and climatic conditions [4, 5]. Given its economic and cultural importance, its genome is relatively well known, specially compared with other Mexican plants. The maize genome, which was first published in 2009 [6, 7], consists of ten chromosomes, and has an extension of ca. 2.3 gigabases, comprising 32,590 genes clustered in 11,892 families. In addition, almost 85 % of the maize genome is composed of different families of transposable elements, which were initially described in this crop.

As we mentioned above, maize was domesticated in Central Mexico, 11,000 to 9000 years ago from their wild relatives, commonly called teosintes in scientific literature [1, 8, 9]. Although some experts are not convinced by the subspecies nomenclature (see [10]), currently three subspecies of teosinte closely related to maize are usually recognized. The Balsas teosinte, *Zea mays* subspecies *parviglumis* (from now on *parviglumis*) Iltis et Doebley, mainly growing in the Balsas river basin and in the state of Jalisco including also a population in southern Oaxaca. *Parviglumis* is adapted to growth at low elevations in tropical seasonal (with marked dry season in winter) regions, between 340 and 1929 m.a.s.l. at an average of 1058 m.a.s.l. [5]. The ethnobotanical information about this subspecies is scarce. However, besides being used for cattle consumption, there is a report of medicinal use [2], in which seeds are imbibed in water and consumed for stomach pain. Also, Mondragon-Pichardo and Vibrans [2] report people who have heard that crossing *parviglumis* with maize during many generations hardens the maize kernel. The second subspecies is the highland teosinte *Z. m.* spp. *mexicana* (Schrader) Iltis. (from now on *mexicana*) that grows in the volcanic region of central Mexico, at higher altitudes, at elevations between ca. 2000 and 2600 m.a.s.l., with an average of 2105 m.a.s.l., in colder, drier regions, and generally more variable temperatures [5]. Although both subspecies are mainly allopatric, both overlap in sites of northern

Balsas River Basin, where they occasionally hybridize [11]. Finally another subspecies, *Z. m. huehuetenangensis* is found only in populations in western Guatemala, near its border with Mexico, and it has been shown that this taxa is a more distant relative to the two other teosintes subspecies and to the cultivated corn [11].

In this Chapter, we review the genetic resources and phylogeography of maize and its wild relatives, *Z. m.* ssp. *parviglumis* and *Z. m.* spp. *mexicana*, discussing traditional and current ideas on the origin, spread and improvement of maize, using recent genomic and molecular evolution information.

The Evolutionary Biology and Ecology of Teosinte and Maize

Zea is divided into two sections, *Luxuriantes* and *Zea* [1]. The *Luxuriantes* section is characterized by ruderal species adapted to disturbed environments that includes *Z. luxurians*, an annual diploid species that grows in Guatemala and Nicaragua (although the Nicaraguan populations were reclassified as *Z. nicaraguensis* by Iltis and Benz [12]); *Z. diploperennis*, which is a perennial diploid species that is principally found in the Jalisco state and used for cattle consumption during the dry season [13]; and *Z. perennis*, which is a perennial tetraploid species also found in Jalisco. Sánchez et al. [14] described some teosintes populations within the *Luxuriantes* section as having morphological, ecographic, cytological, and molecular traits that suggest they may represent new species. The first one is a perennial diploid population from Nayarit, another one, a perennial tetraploid population from Michoacán, and the third one a diploid annual plant from Oaxaca.

On the other hand, *Zea* section is composed exclusively by diploid taxa, and includes the cultivated maize (*Z. mays* ssp. *mays*), the two teosintes mentioned above (*Z. mays* ssp. *mexicana*, and *Z. mays* ssp. *parviglumis*), and the subspecies *Z. mays* ssp. *huehuetenangensis*, found in a few populations in eastern Guatemala. Using molecular data (26 nuclear loci), the divergence between *luxurians* and *parviglumis* was dated 140,000 years ago, and the divergence between *Z. m. mexicana* and *Z. m. parviglumis* at 60,000 years ago [15]. Afterwards, teosintes and maize have experienced subsequent demographic expansions that resulted in their actual high levels of genetic variation [15]. *Zea. mays* ssp. *mexicana*, and *Z. mays* ssp. *parviglumis* are genetically and evolutionary very close, as demonstrated by the number of intermediate and admixed populations and genotypes [8, 9, 11].

Recent genetic studies suggest that *Z. m. parviglumis* is the ancestor of the cultivated maize [8, 9, 15], as we will explain below. However, *mexicana* can be very similar to cultivated maize, but this has been interpreted as a result of subsequent introgression with maize after domestication [9, 16].

Obviously, since teosintes are the wild ancestors of maize, understanding their evolutionary biology is important. Besides, given their abundance, their high genetic diversity [15], and the diversity of environmental, ecological, and edaphic conditions in which they grow [5], teosintes are ideal for the study of population genetics and for understanding the basis of adaptation. Finally, given the synteny (the conserved order of the genes in the chromosome) between maize and teosintes and its evolutionary closeness, genomic data, and genetic tools developed for maize can be used most of the times in teosintes.

The recent studies in teosintes have undergone a gradual improvement in the nature of the genetic markers used, in the number of loci, populations and individuals analyzed, as well as a shift to wild population-based studies with larger sampling numbers, in contrast to the original studies, where few individuals per accession from a seed collection were used (i.e., [8, 11]). For instance, using 93 microsatellite nuclear loci, Fukunaga et al. [11] conducted a genetic analysis of 237 plants obtained from 172 accessions (collection sites) of the wild subspecies *mexicana*, *parviglumis*, and *huehuetenanguensis*, as well as Z. *diploperennis*, *Z. luxurians y Z. perennis*. In general, *Z. m. parviglumis* has a higher genetic diversity than *Z. m. mexicana*. A phylogenetic analysis suggests that *mexicana* was originated from *parviglumis*, and that together they form a monophyletic group. This study, as is the case of others that analyze cultivated maize (i.e., [17, 18]), was conducted using accessions, which has the limitation that it is not possible to determine accurate genetic frequencies and therefore it is difficult to conduct detailed population genetic and phylogeographic analyses.

Using 61 populations (45 populations of maize described in [19] and 16 teosinte populations from [20]), Buckler et al. [21] analyzed with 21 isoenzymes 9 to 50 plants per population. According to this study, *Z. m. parviglumis* is basal and paraphyletic, including *Z. m. mexicana* as a monophiletic clade (supporting the results of 11). In addition, they reported that *Z. m. huhuetenanguensis* is basal to the other taxa, and sister taxon to the other two. Finally, these authors analyzed the phylogeography of teosintes using chloroplast RFPLs, finding five haplotypes (four in *parviglumis*, three in *mexicana* and two shared haplotypes). Although their results do not show a high resolution, they found isolation by distance, and some isolation generated by altitude, perhaps related to the climate.

Merino-Díaz [22] analyzed in average 27 individuals in 10 populations, which covered most of the distribution of both subspecies. He obtained 139 ISSRs polymorphic loci, which are nuclear dominant markers related to microsatellites [23]. With these markers, he found a mean diversity of $H_S = 0.261$ and a mean polymorphic variation of 77.74 %. This diversity is high compared, for instance, to the genetically diverse species of the *Agave* genus found in Mexico, that in average have a lower mean genetic diversity (33 studies $H_S = 0.19$) and a lower mean polymorphic diversity ($P = 56$ %; [23]). In addition, [22] found a high genetic differentiation among populations ($\theta_{\mathrm{WC}} = 0.1837$, $\theta_{\mathrm{H}} = 0.23$) using, respectively, the Weir and Cockerham theta [24] and the Hickory bayesian estimation [25, 26]. Given that teosintes are wind and cross-pollinated, their genetic differentiation would be expected to be low [27, 28], but it was higher than, for instance, the average found in the animal pollinated *Agave* genus (23 studies, $F_{ST} = 0.15$; [23]). Of the 139 loci, Aguirre-Liguori et al. (in prep) identified with Bayescan V.2 [29] three loci that appear to have been under directional selection and one additional locus that shows evidence of balancing selection. We analyzed the correlation between genotype frequencies of the three loci that appear to be under directional selection and their population environmental data, and found that two are associated with altitude, suggesting local adaptation. Although ISSRs are anonymous markers, we suggest that this approximation will help us to detect complex patterns of genetic adaptation and genetic structure.

Villasante-Barahona [30] amplified nine nuclear microsatellites in 26–37 individuals from five populations of both subspecies, detecting, not surprisingly, higher levels of genetic variation than those estimated with ISSRs—as it generally occurs with microsatellites, given their high mutation rate and high number of alleles. Mean population diversity ranged from $H_S = 0.727$ to 0.807 and a number of alleles that ranged from 5 to 23. Comparing this data with an *Agave* (*A. parryi* average $H_S = 0.621$, 4 loci [31]) indicates again that teosinte is genetically very diverse, consistent with [15]. This study reported low F_{ST} values for pairs of populations (from 0.0389 to 0.139). However, it was interesting that he found significant and positive F_{IS} values (range 0.103–0.219), given the species is wind pollinated and has monoecious flowers. This suggests there is inbreeding; either originated by selfing and/or crosses with relatives, or generated by genetic structure within the sampled populations (i.e., Wahlund effect). In order to answer this question, it is essential to study the mating systems of wild populations along the patterns of gene flow within populations with detailed paternity analyses.

Moeller et al. [32] used five nuclear genes and two chloroplast sequences to analyze *Z. m. parviglumis* using 84 individuals in seven populations (four in Jalisco and three in the Balsas region). The Balsas region had more genetic variation than the Jalisco region, and an AMOVA showed that the majority of the differentiation was found within regions. Analyzing the chloroplast, they found a strong phylogeographical structure, but not clear patterns, with many populations presenting a unique haplotype confined to a single region. However, they found evidence of gene flow through seeds between regions.

In detailed analyses of two Balsas basin *parviglumis* populations [33] used 468 SNPs in 389 and 575 individuals in two populations finding similar levels of genetic diversity in both sites, and a low genetic differentiation between them. However, the genomic resolution allowed them to detect low, but significant genetic structure within each site that could be correlated to the sites environmental and topographic heterogeneities. This study is interesting since it shows a complex and fine genetic structure in teosintes, despite being wind pollinated, as well as the power of resolution achieved using numerous genetic markers.

Pyhäjärvi et al. [34] increased considerably the number of loci to more than 36,000 SNPs, and studied 250 individuals that belonged to 21 teosinte populations (11 from *parviglumis* and 10 from *mexicana*). These populations covered most of the distribution of the subspecies. These authors found that teosintes present hierarchical genetic structure [35], which means that populations within a neighborhood present more gene flow than population between neighborhoods. Using different methods [34] found numerous SNPs associated to environmental variables. Interestingly, several SNPs that had a signal of selection were in intergenic spacers or were synonymous. In addition, they identified four large regions with high linkage disequilibrium (more than 10 million base pairs) that might correspond to inverted regions in the genome that inhibit recombination. These regions are rich in SNPs that are statistically associated with temperature and altitude. Among the inversions found, one (*Inv1n*) was at mid frequencies in low altitudes and at low frequencies at higher altitudes. Another one (*Inv4n*) was exclusively found at high altitudes in both subspecies, suggesting that it is relevant for high altitude adaptation. A third inversion was exclusive to the highest populations of *mexicana*.

Fang et al. [36] analyzed the *Inv1n* inversion, which corresponds to 50 Mb found in Chromosome 1, with 941 SNPs from 542 mapped genes. This inversion has a high linkage disequilibrium (i.e., some allelic combinations are more frequent that what is expected under total random recombination) compared to the rest of the chromosome. However, when they analyzed the linkage disequilibrium within the inversion, they found similar values compared to the rest of the chromosome, suggesting that recombination occurs within the inverted region. The inversion divides *parviglumis* into two distinct groups that are not detected in the rest of the chromosome. They also sequenced four loci within the inversion region that support their results. The inversion diverged between *parviglumis* and *mexicana* at the same time, indicating that it is not from an introgressed origin and estimated the divergence time of the inversion at ca. 300,000 generations. This time predates the divergence between *Z. luxurians* and the ancestor of *parviglumis*, suggesting that it was lost by genetic drift in the other taxa, perhaps because of their smaller effective population size. Finally, as this inversion is not found in maize (even if it was domesticated from *parviglumis*), the authors suggest it was lost due to selection against the inversion. To test whether the inversion is adaptive, these authors correlated their frequency with environmental variables, and found negative but significant associations with altitude and some associated climatic variables.

As is the case of inversions, other types of genome architecture changes can influence local adaptation. These are non-codifying but functional elements, such as transposable elements (TE), heterochromatic knobs, or copy-number variants and presence/absence polymorphisms [37]. Transposable elements were first described in maize [38], and there have been recent improvements in understanding their role in the evolution of genome size, and their effects on fitness.

Transposable elements are interesting because there are many families that behave differently in the genomes, in terms of where they insert themselves, either doing it in genic or non-genic regions. Given their nature, transposable elements dynamics in the genomes are normally regulated by purifying selection, explaining for instance why animals that have high effective population sizes tend to have fewer transposable elements [39]. Using Next Generation Sequencing (NGS), which are approaches that allow genomic-wide sequencing, Tenaillon et al. [40] analyzed the TE components of *Z. mays* (B73) and *Z. luxurians*, and compared their genome sizes (GS). These authors found that maize has a 1.5 fold shorter genome compared to *Z. luxurians*, which is in part explained by differences in abundance of TE. According to their results, TE explains 70 % of GS differences between *Z. luxurians* and maize, with the former presenting more TE families and abundance than the latter. These differences could be associated with changes in physiology, phenology, and life history traits [41]. Although there could be purifying selection against transposable elements, which could explain their reduction in maize, there are families that discriminate where they insert themselves, such as the *Class 2 miniature inverted repeat elements* (MITEs). These transposable elements are able to insert themselves in genic regions, which could affect the functioning of genes or change their regulation mechanism, and may help in some cases to adapt.

Chia et al. [37] analyzed the genomic diversity of 103 inbreed lines including elite inbreed lines, landraces, and teosintes, for a total of 55 million SNPs. Twenty-one percent of the SNPs were associated with genic regions (825,000 synonymous and 571,000 nonsynonymous, and 10,000 were non-sense). In the case of the *Zea* section, these authors found that heterochromatic knobs correlated positively with GS, while in an apparent paradox, transposable elements abundance correlated negatively with GS. This means that while there has been a reduction in GS associated with loss of heterochromatic knobs (probably through purifying selection), there has been an increase in the number of TE. Overall, the data [37, 40] suggest that transposable elements are responsible of GS variation in grasses, but in maize there has been a shift to a major variation associated with heterochromatic knobs.

Diez et al. [42] found that GS in teosinte and maize varies among populations and within populations, and correlates with environmental variables, suggesting it could be under selection. Diez et al. [42] analyzed and compared the GS of 5 individuals from 21 populations of both subspecies of teosintes and 22 Mexican traditional landraces, which were distributed at diverse environments, at altitudinal clines and at two parallel transects. If the sequenced maize B73 is used as a reference (i.e., GS = 1), a significant variation in GS among individuals (ranging from 0.948 to 1.299) and a difference in average GS between maize (1.095) and teosinte (1.129) is found, although both groups had a similar coefficient of variation. Most variation occurred among populations for both groups, but it was higher in maize. In particular, we found a stronger reduction in GS for inbred elite lines, suggesting that there has been a reduction in GS, associated with domestication [40]. Two gradients were studied for each group. For the teosintes, we sampled gradients in the Balsas and Jalisco region and for maize in the Balsas and Oaxaca gradients. When we considered these gradients, we found a significant variance caused by the gradients for both groups, but it was higher for the cultivated maize. When we compared the GS variation, an association between bioclimatic (temperature and precipitation) and geographic (latitude and longitude) variables and GS in the Balsas gradient of maize samples (while it was not significant for the Oaxaca gradient) was detected. In the case of teosintes, only some variables, which were associated with seasonality variables (precipitation in the warmest and coldest quarters), were significantly correlated with GS. For maize, we also found an association with geographic coordinates, which could reflect complex environmental or cultural scenarios. Overall, these results suggest that GS evolves in complex ways with different selection pressures and/or random process changing GS in alternative ways.

The Domestication of Maize and the Problem of Introgression Teosinte-Maize

Given the importance of maize and the high diversity of landraces, there have been many efforts to identify the origin of maize. Many hypotheses have been developed to answer this question. For a recent review on traditional hypothesis, see [1]. However, with the development of molecular analyses it has been possible to advance in answering this question, although the results are not as straightforward. It is important to consider that given the strength of selection that occurred during maize domestication, comparing wild and domesticated maize has allowed to start understanding the genetic basis of adaptation, as well as the processes that have been involved [43].

As it has been pointed out earlier in this chapter, maize and teosinte are characterized by their enormous genetic and phenotypic diversity, which has led to hypothesize that it was domesticated multiple times, as it has occurred in other crops. In an effort to determine the origin of maize, Matsuoka et al. [8] used 93 microsatellite markers and 264 individuals of teosinte and maize that cover a broad distribution. According to their phylogenetic analyses, they found strong support (930 out of 1000 bootstrap samples) that maize was domesticated only once from *parviglumis*, thus making maize monophyletic. In addition, they dated the origin of maize around 9188 years BP, with a 95 % confidence limits ranging from 5689 to 13,093 years BP. Using a principal component analysis, they clustered different groups of maize and teosintes, finding that *mexicana* is separated from maize, supporting the evidence that *parviglumis* was the only ancestor of maize. When trying to identify the closest ancestor to maize, they found that *parviglumis* of the central region of the Balsas River is the closest candidate, and placed the domestication in central Oaxaca (although they suggested that a finer sampling would help defining better the site of domestication). Also, they detected admixture between subspecies, and notably introgression from *mexicana* into maize, explaining (at least in part) the high genetic and morphologic diversity encountered and the adaptation of the highland maize. Finally, the genetic clusters identified by Matsuoka et al. [8] suggest that the initial diversification of maize occurred in the highland landraces, and originated two main lineages, one that dispersed to the North of Mexico and North America, and the other one that dispersed to the western and southern lowlands of Mexico and subsequently to the Caribbean, Central and South America. There are opposite archeological and genetic evidences that place the diversification of maize at different altitudes, suggesting that either maize diversified in the highlands and subsequently spread to the lowlands, or that maize from the lowlands was first domesticated and then rapidly diversified into the different landraces, particularly in the highlands; see review in [5].

In particular, most genetic data suggest that primitive maize landraces that grow in the highlands are more similar to *parviglumis* than maize that grow in lowlands, and that they are also the ancestors to the rest of the cultivated maize. In an attempt to unravel this paradox, van Heerwaarden et al. [9] used 964 SNP from 547 genes in 1127 accessions of maize landraces in addition to more than 100 accessions of *Z. m. parviglumis* and 96 of *Z. m. mexicana*. Using a principal components analysis (PCA), they concluded that *parviglumis* is closer to maize landraces. However, they found similar genetic patterns among highland races and *mexicana*. In addition, they found admixture among the three subspecies, and particularly strong between *mexicana* and the highland races. Given that admixture between ancestral maize and teosintes could affect the genetic signals, these authors used a method that attempts to estimate the ancestral allele frequencies of maize. When they compared the estimated ancestral frequencies of maize with those of the maize landraces, they found that the closest frequencies were those found in the west of Mexico lowland landraces. van Heerwaarden et al. [9] concluded that maize was thus domesticated in the lowlands, and subsequently diversified into other landraces. To explain the apparent paradox mentioned above, these authors proposed that the maize highland races had strong admixture with *mexicana*, which introduced many teosintes alleles into the maize gene pool, making them genetically more similar to teosintes. For example, the palomero toluqueño, a highland race, seems to have an important proportion of *mexicana* genome [8]. Overall, this study shows that, either introgression can mislead our inferences, or that we still know little about the true origin of maize.

Recently, Hufford et al. [16] analyzed the putative introgression between *mexicana* and maize. These authors analyzed nine sympatric *mexicana* and maize populations and one isolated (allopatric) *mexicana* population, using 189 individuals and 39,029 SNPs. Although maize and teosintes have well-defined genetic "membership," there is important admixture in the sympatric populations. However, they found that gene flow is asymmetric, with *mexicana* contributing more to the gene pool of maize, and that apparently this process is ancient (ca. 174 generations in maize according to a likelihood of introgression analysis). In addition, Hufford et al. [16] studied the genomic regions that were introgressed and found that within these regions there are many shared SNPs, and were more similar to the non-introgressed regions of the taxa of origin, suggesting similar evolutionary histories, i.e., that introgressed regions in maize had similar diversity than *mexicana* genome. When comparing introgressed and non-introgressed regions, they found that introgressed regions were not rich in domestication genes, but were associated with local adaption to highlands, such as genes associated with pigmentation and macro-hairs, which are important in adaptation to cold and higher lands [34]. When Hufford et al. [16] analyzed the introgressed parts of *mexicana*, they did not find genes associated with domestication, suggesting that *mexicana* has resisted the gene flow from these genes and indicating that *Z. m. mexicana* has always been adapted to disturbed environments, as it happens for species of the section *Luxuriantes*. This resistance to gene flow from domesticated genes could happen either because gene flow from maize to *mexicana* is rare, and probably not advantageous; or that humans could select against *mexicana* hybrids that present intermediate phenotypes. However, the fact that *Z. m. mexicana* is adapted to disturbed environments suggests it might be the true ancestor of maize, and thus the similarity between highland races and *mexicana* could be explained by this alternative hypothesis. In order to have a definitive test if there is ongoing introgression from *mexicana* into maize, and its magnitude, it would be necessary to analyze with paternity tests the contribution of each subspecies to new seeds. Furthermore, it would be interesting to introduce in experimental fields, lowland maize and highland teosintes and evaluate if adaptive introgression to highlands occurs.

The current distribution of teosinte *Z. m. mexicana* and *parviglumis* is mainly allopatric, and mostly determined by altitude, precipitation, and temperature [5]. There are a few geographic regions were they overlap and where there seems to occur gene flow [11]. In contrast, as mentioned above, cultivated maize as a total has a wider niche, giving its current and extended distribution, varying in elevation, temperature, and seasonality; but each race and variety has its own adapted environmental conditions [4, 5].

We have already reviewed the current ideas and data on the origin and phylogeography of teosintes and maize; however, little is known about the environmental context in which they occur. Using niche modeling, we analyzed the change in potential distribution of these subspecies, as well as four ancestral landraces, to determine how its ecological history has changed [5], in general supporting the genetic analyses we previously described, while helping to determine the climatic environments where domestication took place. The study of [5] used the MaxEnt program and a set of 19 bioclimatic variables to analyze the current potential climatic niche distribution, the potential niche during the Last Glacial Maximum (LGM), 21,000 years ago—when temperature was 4 to 6 °C cooler and 10–30 % drier that today—and during the Last Interglacial (LI), 135,000 years ago. Paleoclimatic evidences suggest that there were important climatic shifts, and particularly at 10,300 and 8200 years ago, resulting in important vegetation shifts during the time of domestication. This has made it difficult to determine the climatic context during domestication and the past distribution of the wild taxa. The analyses indicated in general terms that while *mexicana* is able to grow in a wider diversity of environments, *parviglumis* is confined to a more tropical and seasonal temperature and precipitation. According to our niche modeling, there was an important increase in the distribution from the LI to the LGM, and a minor increase to the present time, suggesting a continuous population increase of teosintes populations, as inferred previously [15]. In addition, we found that *parviglumis* has apparently expanded into higher areas, a shift from 524 m.a.s.l. to the current mean of 1058 m.a.s.l., while *mexicana* changed from a mean altitude of 1836 m.a.s.l. to the current average of 2015 m.a.s.l. 21,000 years ago (at the LGM). Given these results, we proposed that *parviglumis* colonized the Central Balsas region, while *mexicana* expanded through the Transverse Volcanic Axis and into the state of Oaxaca. Since the LGM, *parviglumis* expanded to Nayarit, Northern Jalisco, and Eastern Guerrero, and *mexicana* increased its geographic range to the State of Mexico, Tlaxcala, Puebla, and Oaxaca. We found areas of overlap in the three models, which could correspond to potential Pleistocenic refugees and in consequence these areas may be richer in genetic variation, and relevant sites of field study for the understanding of maize domestication. For *parviglumis*, the proposed refugia are in Michoacan and Colima, in the border with Jalisco, while in *mexicana* we identified a similar area in Jalisco and the north of Michoacán.

Hufford et al. [5] also analyzed the potential climatic niche of several traditional and putatively old landraces including Arrocillo Amarillo and Palomero Toluqueño from the highlands and Nal Tel and Chapolote from the lowlands, finding that their distributions have expanded beyond the distribution of their wild relatives, showing that maize adapted to novel environments since its origin and that the diversification process was very fast. This may explain why there are so many old archeological vestiges found outside the distribution of *parviglumis*, which makes it difficult to determine where they were domesticated. An alternative hypothesis is that it was domesticated from an ancestor of the recent *parviglumis* and *mexicana*, but perhaps more closely related, in climatic adaptations, to the current *mexicana* genomes.

From the above sections, it is clear that the vast diversity of maize was shaped by strong natural and artificial selection, coupled by huge effective population sizes allowed by its out crossing, open pollinated system. There was first a domestication process followed by an improvement process that occurred according to the necessities of the environments in which maize was selected. With the recent development of genomic analysis, it has been possible to determine the genes associated with domestication and improvement. For instance, Hufford et al. [44] analyzed over 21 million SNPs in the genomes of 35 improved lines, 23 land races, and 17 individuals of both subspecies of teosinte. Comparing teosintes, traditional landraces of maize and elite recently derived inbreed lines, 484 genetic regions associated with domestication and 695 genetic regions associated with improvement were suggested. In addition, the intensity of selection was estimated to have been, in average, stronger during the domestication process (a selection coefficient $s = 0.015$), than during the improvement process ($s = 0.003$). It has been an important objective to determine which genes were involved first in domestication and in later improvement processes. In particular, several genes associated with domestication have been identified, some previously well known (*tb1)*, and some other worth of carefully analyzing their population genetics [44]. After domestication and initial development of traditional landraces by Mesoamerican people, there was a subsequent weaker selection in the improved lines used in the USA, on many genes already associated with domestication, highlighting the importance of this old landraces in the actual and future improvement of maize [9]. Besides, Hufford et al. [44] determined the genomic basis of features associated with both domestication and improvement. They found that domestication features contained in average 3.4 genes that covered 322 kilo-base pairs and 7.6 % of the maize genome. On the other hand, traits associated with improvement were in average smaller, and involved fewer genes.

Although domestication occurred through selection on genes, it can also occur through changes in transcription. In the case of maize, phenotypic change from the ancestor has been substantial, which suggests that there should be differences in transcription or in transcription networks. In order to answer this, Swanson-Wagner et al. [45] used an array that covered over 18,000 expressed genes to see differences in gene expression and gene co-expression between 24 accessions of wild relatives and 28 of cultivated maize. The eight days plants profile (i.e., basal transcripts) showed that there is not a whole genome change in transcripts between wild and domesticated lines, indicating that domestication and improvement did not shift in general the expression. However, they found 612 genes that had a significant differential expression between *parviglumis* and maize and from these, 288 had a two-fold difference, with a slightly general higher expression in maize. Interestingly, these differences were not fixed for subspecies, but instead different lines shared teosinte like-expression and vice versa. Nevertheless, adaptation can occur not only because of differences in expression, but also because of changes in co-expression, which means that two or more genes are expressed simultaneously, resulting in a genetic network interaction. Comparing the topologies of co-expression, they found a significant change in gene network during domestication. In total, they identified 1115 genes with altered co-expression, from which only 276 of these also had differences in expression. When they compared the expression of genes with the traits of domestication and improvement identified by Hufford et al. [44], for many there were increases in expression and changes in co-expression, although only the former were significant. In general, it was found that genes that had a change in expression were higher in maize, although they had a better connectivity (co-expression) in teosintes. The limitation in this study is that they used plants at the initial grow, and not older tissues that could be more easily associated with domestication traits (i.e., ears or flowering time). Nevertheless, it is interesting to see that they found important differences in plants that had similar morphologies.

According to Hufford et al. [5], different races and populations of maize and teosinte are sensitive to patterns of seasonality and temperature. Taking this as guidance, it will be relevant to determine genes of agronomic importance for tolerance (weather, plagues) and improvement (increase in size) in both cultivated and wild relatives to define strategies that will help respond to climate and global change.

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Chapter 17
Chile Peppers (*Capsicum* spp.)

Barbara Pickersgill

Abstract Most Mexican chiles belong to the species *Capsicum annuum*. Domesticated types of *C. annuum* are derived from wild *chile piquin*, currently suffering genetic erosion as a result of habitat loss and over-exploitation. It is consequently now difficult to determine where or how often *C. annuum* was domesticated. The only trait consistently distinguishing wild from cultivated *C. annuum* is rate of germination. Other traits of the domestication syndrome, such as fruit size, position and loss of dispersal, vary among landraces. Diversification traits are usually attributed to human selection after domestication and include fruit shapes, colour and degree of pungency. Some domestication and diversification traits are controlled by major genes, others by several to many quantitative trait loci. Much of the diversity in Mexican chiles was present by the time of the Spanish Conquest and probably reflects selection for different uses in cooking, as markers for invisible qualities such as flavour, or simply for aesthetic reasons. The archaeobotanical record is too limited to show where or in what order domestication and diversification traits arose. Remains (mainly seeds) are present from the earliest phases of caves in the Tehuacán valley, but all seeds from preceramic levels are within the size range of modern wild *chile piquin*. The earliest convincing evidence of domesticated chiles follows a gap of over 1500 years in the archaeological record. Aztec tribute lists show that impressive quantities of chiles were being produced at the time of the Conquest. Accounts by the chroniclers demonstrate that different colours, shapes and degrees of pungency of the fruits were established and used in a variety of stews and casseroles, in medicine, and as a punishment. Today chiles are used fresh (for example, *jalapeño*, *serrano* or sweet pepper) or dried (for example, *pasilla* or *mirasol*). Concerns about genetic erosion have prompted studies on the distribution of genetic variation in wild and cultivated populations and led to recommendations for collecting for ex situ conservation. More work is needed on the role of local people in conserving diversity in situ, in farms and/or home gardens.

Keywords *Capsicum annuum* • Domestication • Diversification • Major gene characters • Quantitative trait loci • Archaeological record • Genetic erosion • Conservation

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In 1529, less than a decade after the surrender of the Aztec capital Tenochtitlán to the invading Spaniards, the Franciscan friar Bernardino de Sahagún arrived in Mexico. He learned Nahuatl, the language of the Aztecs, and started to record details of the daily life of the Aztecs, as told to him by his native informants [1]. Publication of his multi-volume *Historia de las Cosas de la Nueva España*, written in Nahuatl and Spanish, was suppressed by Philip II of Spain, but the manuscript survived and was rediscovered in the late nineteenth century [2]. Sahagún gave a vivid description of the chiles sold in the market of Tenochtitlán: "… mild red chiles, broad chiles, yellow chiles, *cuitlachilli*, *tempilchilli*, *chichioachilli*. [The chile seller] sells water chiles, *conchilli*; he sells smoked chiles, small chiles, tree chiles, thin chiles, those like beetles. He sells hot chiles, the early variety, the hollow-based kind. He sells green chiles, sharp-pointed red chiles, a late variety… Separately he sells strings of chiles, chiles cooked in an *olla*, fish chiles, white fish chiles" [2]. Sahagún also listed the dishes in which these chiles were used: "one kind of casserole of fowl made in their fashion, with red chile and with tomatoes, and ground squash seeds, a dish which is now called *pipián*; they ate another casserole of fowl made with yellow chile … They also ate many kinds of chile stews; one kind was made of yellow chile, another kind of *chilmolli* was made of *chiltecpitl* and tomatoes; another kind of *chilmolli* was made of yellow chile and tomatoes. They also ate fish in casseroles: one of white fish made with yellow chile and tomatoes; another casserole of greyish-brown fish made with red chile and tomatoes, and with ground squash seeds which is very good to eat. They eat another kind of casserole made of frogs with green chile; another kind of casserole of those fish which they call *axolotl* with yellow chile; they also ate another kind of tadpoles with *chiltecpitl*. They also ate a kind of little reddish fish made with *chiltecpitl*; they also ate another casserole of large winged ants with *chiltecpitl* … they also ate maguey worms, with *chiltecpitl molli*; also another casserole of shrimps made with *chiltecpitl* and tomatoes, and some ground squash seeds … they ate another casserole made of unripe plums [*Spondias*], with some little white fish, yellow chile and tomatoes" [2]. Elsewhere Sahagún described the sauces on sale in the market, made with smoked chile, hot chile, yellow chile, mild chile, green chile or an early variety of chile. He classified the sauces as "picante, muy picante, muy muy picante, brillantemente picante, extremadamente picante, picantísima" [1]. It is apparent from Sahagún's descriptions and from Dr. Francisco Hernández's less comprehensive account of seven different chiles used by the Aztecs, written about 1615, that much of the diversity associated with Mexican chiles today was already in existence before chiles became known to Europeans and long before the start of modern *Capsicum* breeding.

To gain some understanding of how this diversity originated and is maintained, it is necessary to review the taxonomy of the genus *Capsicum*, the wild ancestors of the Mexican chiles and the changes resulting from domestication, the archaeological record insofar as this enables these changes to be dated, and the interactions of people and peppers that have partitioned diversity into different types of chile, often with different uses.

Taxonomic Background

The genus *Capsicum* originated and initially diversified in South America. At least three species were domesticated independently in that continent, from wild ancestors that were clearly distinct species: *C. baccatum* from conspecific wild forms in the Andes of Peru and/or Bolivia; *C. pubescens* also in the Andes, from an unknown wild progenitor probably related to *C. eximium* and *C. cardenasii*, both of which are endemic to Bolivia; and *C. chinense* probably in Amazonia, where conspecific wild forms have recently been reported from the Brazilian state of Roraima [3].

Two of these three South American domesticates have reached Mexico, both apparently relatively recently. *Capsicum pubescens* is the most cold tolerant of the domesticated species. It is easily recognised by its pubescent foliage, purple flowers and thick-walled fruits with distinctive dark brown to black seeds. In Mexico it is most commonly known as *perón* or *manzano* (apple), but sometimes as *ciruelo* (plum) or *jalapeño* [4]. It is always eaten fresh because the thick fleshy pericarp prevents the fruits from being dried satisfactorily. Laborde and Pozo [4] considered that there had been only a single introduction of this species, said to have occurred between 1930 and 1940 [5], because they found very few differences between accessions collected from various remote and isolated localities in highland Mexico. This species will not be discussed further here.

Unlike *C. pubescent* ;*C. chinense* is adapted to hot humid climates. In Mexico, it is associated particularly with the Yucatán peninsula. It is known as *chile habanero*, which suggests that it may have reached Mexico from Cuba. It is the only chile found in Yucatán that has no Mayan name, which also suggests that it was introduced rather than indigenous [4]. Before the twentieth century, the Yucatán peninsula had more trade with Cuba than with the rest of Mexico [4] and *C. chinense*, particularly forms with the Scotch Bonnet fruit shape characteristic of *habanero*, are widespread in the West Indies. *Habanero* fruits are valued for their characteristic aroma as well as their pungency, and are now finding a specialty market outside the American tropics. They are always used fresh. Like *C. pubescens*, *chile habanero* will not be discussed further here.

Capsicum chinense is very closely related to *C. annuum* and *C. frutescens*, which together include the remaining Mexican chile peppers. Numerical taxonomic studies of morphological variation suggested that domesticated *C. annuum*, domesticated *C. frutescens* and domesticated *C. chinense* originated independently from different elements of a geographically widespread and morphologically variable complex of wild and weedy peppers distributed from the southern United States through Mexico and Central America south to northern South America [6]. This scenario was supported by a subsequent study of the DNA polymorphisms known as microsatellites [7]. The phylogenetic tree constructed from the microsatellite data showed that some accessions of wild *C. annuum* were basal to the branches comprising domesticated *C. annuum*, while others were positioned at the root of the branches containing, respectively, *C. frutescens* and *C. chinense*. Although the three domesticates can usually be distinguished from one another with reasonable certainty, the wild forms intergrade, so are often difficult to assign to a particular species. Crosses between the domesticates and among wild accessions often have reduced fertility [8, 9], resulting from heterozygosity for chromosome structural rearrangements, mostly reciprocal interchanges. These hybrids may also show varying degrees of sexual sterility and morphological abnormality apparently resulting from disharmonious nuclear-cytoplasmic interactions. The sterilities combine with geographic isolation to restrict gene flow within this complex of wild and domesticated peppers.

Opinions differ on what rank to assign to the wild versus domesticated peppers, and whether to recognise one species or three in this complex. Wild *C. annuum* has been treated as taxonomically distinct from domesticated *C. annuum* at the level of variety, but the scientific name of the wild variety has been subject to many changes for nomenclatural reasons. The uneuphonious *C. annuum* var. *glabriusculum* is becoming generally accepted, though the synonyms var. *aviculare*, var. *minimum* and var. *baccatum* may all be found in the literature. All cultivars and landraces of domesticated *C. annuum* are included in var. *annuum*. Comparable taxonomic recognition has not been given to wild versus domesticated *C. frutescens* or *C. chinense*.

Since domesticated *C. annuum*, domesticated *C. frutescens* and domesticated *C. chinense* differ genetically in some significant respects and incorporate different elements of the gene pool represented by the complex of wild peppers, *Capsicum* breeders have generally found it convenient to retain the three species. Domesticated *C. frutescens* is mostly found south of Mexico, for example, in Guatemala, Costa Rica and Panama. The species is best known for including the pepper that is the main ingredient of Tabasco sauce, though it is unclear whether this pepper came originally from the Mexican state of Tabasco. According to Andrews [10], seeds of a small-fruited, very pungent pepper were given to Edmund McIlhenny by a friend who had served in the Mexican War, were grown on his plantation on Avery Island, Louisiana, and survived abandonment during the American Civil War. McIlhenny subsequently used the fruits as the base for a fermented hot sauce. Demand for this sauce has increased so much that the McIlhenny Company has expanded cultivation of Tabasco pepper to Mexico, Honduras, Colombia and Venezuela, but the company furnishes all the seed to be grown and maintains strict control to keep the pepper true to type [10].

Domesticated *C. annuum* is better adapted to the highland environment than *C. frutescens*, but is prone to attack by pests and diseases in the humid tropical lowlands. It includes the overwhelming majority of Mexican chiles and is also by far the most economically important species on a world scale. It is consequently the most intensively studied species of *Capsicum* with regard to diversity, domestication and genetics. The remainder of this chapter therefore relates principally to *C. annuum*.

Chile Piquín and the Region(s) of Domestication of *C. annuum*

Wild *C. annuum* is known as *chile piquín*, *chiltepín*, *chiltepec* or bird pepper and also has other local names. It is or was found wild in western Mexico from Sonora to Chiapas and in eastern Mexico from Tamaulipas to the Yucatán peninsula [4]. It also occurs in the southern United States, in Arizona and Texas [11]. It has been recorded at more than 2000 m above sea level in the foothills of the Sierra Gorda in Querétaro [11], but usually occurs at lower altitudes. It represents that segment of the wild *C. annuum*–*C. chinense*–*C. frutescens* complex that is morphologically closest to domesticated *C. annuum* [6] and also closest in molecular characteristics [7].

Chile piquín is a perennial plant that eventually forms a small bush. It loses its leaves in cold or dry conditions but resumes growth with the return of favourable conditions [4]. Each plant bears numerous small red fruits in an upright position, so easily visible to birds. The fruits separate easily from their stalks when ripe and are readily removed by birds. Birds are the primary dispersers, and those feeding on wild chiles have been shown to defaecate seeds with unimpaired germinability [12, 13]. Both seedlings and adult plants of *chile piquín* are most common under the shade of nurse trees, particularly those with fleshy fruits, such as hackberry (*Celtis* spp.), in which the birds that feed on wild chiles also forage and roost [14].

Chile piquín characteristically has very pungent fruits, due to presence of capsaicin. Birds differ from mammals in the pain receptors that perceive the pungency of peppers, so capsaicin does not deter bird dispersers [14]. Small mammals such as cactus mice and packrats destroy totally the germinability of any pepper seeds that they consume, so are seed predators not dispersers. However, they avoid pungent fruits [12]. One function of pungency therefore seems to be to protect pepper seeds against predation, but this has a metabolic cost. Tewksbury et al. [15] found that wild populations of three different South American species were polymorphic for pungency, with non-pungency being favoured by selection under certain environmental conditions [16]. Non-pungency has also been reported in wild *C. annuum* [11, 17], though it is not clear whether these reports refer to entire populations or individual plants in a polymorphic population, nor whether non-pungency is favoured by the same conditions as in South America. More field data on *chile piquín* in this regard would be interesting.

Chile piquín fruits have been extensively, and destructively, harvested from the wild to such an extent that many populations are declining or becoming extinct. González-Jara et al. [18] estimated that 50 tonnes per year are harvested from wild plants in central and northern Mexico. The fruits are sold in markets fresh, dried or made into *salsas*. They are considered to have a distinctive flavour and to produce a burning sensation that disappears quickly [4]. Entire branches are cut from the bushes, often before the fruits are ripe, to prevent losses to birds, and the branches are then dried under protection in the house [4]. In addition to damage to individual plants, habitat is being lost as land is ploughed for commercial agriculture. Hernández-Verdugo et al. [19] described isozyme variation in ten wild populations of *C. annuum* from north-western Mexico, but about 12 years later all these populations had disappeared [11]. Similarly, in a study of diversity in relation to region of domestication, Aguilar-Meléndez et al. [20] had to substitute what they called semi-wild populations of *C. annuum* for truly wild populations. González-Jara et al. [18] noted that farmers have now started to grow morphologically wild peppers in monoculture in small traditional fields, probably in order to meet the combination of growing demand and reduction in natural populations.

González-Jara et al. [18] used microsatellite markers to compare genetic diversity and population structure in wild populations, plants left standing in pastures and living fences, and cultivated populations of *chile piquín*. Their results suggested that there was considerable differentiation among wild populations and that gene flow between geographically isolated wild populations occurred via cultivated populations and plants left standing in pastures. The plants left standing did not show any significant loss of genetic diversity compared to wild populations, suggesting little or no human selection in choice of phenotypes to leave in pastures. However, cultivated populations showed a significant decrease in genetic variation. This was attributed to the bottleneck associated with the origin of these populations from a limited sample of wild plants. Insofar as these cultivated populations act as a bridge for gene flow into surviving wild populations, González-Jara et al. [18] suggested that they pose a threat of genetic erosion for wild *chile piquín* additional to threats from habitat loss and over-exploitation.

Erosion of genetic diversity in wild *chile piquín* compromises attempts to locate the region(s) in which *C. annuum* was domesticated by matching variation in the domesticate with variation found in the wild. Wild *C. annuum* was found to show more variation in morphology of mitotic chromosomes (karyotypes) than domesticated *C. annuum* [8]. The karyotype characteristic of domesticated *C. annuum* occurred in accessions of wild *C. annuum* from central and southern Mexico (Sinaloa, San Luis Potosí, Michoacán, Puebla, Oaxaca, Veracruz, Tabasco), whereas north and south of this region accessions of wild *C. annuum* carried the basic karyotype found in all other species of chile pepper. However, some of the accessions of *chile piquín* used in this study were market samples, and González-Jara et al. [18] showed that samples of *chile piquín* purchased in local markets were often not from local populations, so more data are needed in order to map karyotype distributions accurately.

Loaiza-Figueroa et al. [21] found that most members of the *C. annuum*–*C. chinense*–*C. frutescens* complex, including wild *C. annuum* from western and northwestern Mexico, had two genetic loci encoding the enzyme phosphoglucomutase (*Pgm*), whereas domesticated *C. annuum* and wild *C. annuum* from eastern Mexico had three loci encoding this enzyme. They therefore suggested that *C. annuum* was domesticated in eastern Mexico, somewhere between Nuevo León and Tamaulipas in the north and Hidalgo and Veracruz in the south. They also suggested a possible second centre of domestication in west-central Mexico, in the state of Nayarit, though they had no wild accessions from Nayarit to corroborate this suggestion.

Aguilar-Meléndez et al. [20] Studied polymorphisms inDNA sequences in parts of three nuclear genes, using semi-wild populations as proxies for truly wild *C. annuum*. They found greatest diversity among semi-wild populations from the Yucatán peninsula, and suggested that this was a potential centre of domestication. González-Jara et al. [18] found that diversity in microsatellite markers was likewise greatest in populations of wild *C. annuum* from Yucatán and decreased both northwards and westwards. No accessions of wild *C. annuum* from Yucatán were included in the karyotype survey [8], but wild accessions from Yucatán did not show the additional *Pgm* locus (*Pgm3*) characteristic of domesticated *C. annuum* and found also in wild *C. annuum* further north in eastern Mexico [21].

Aguilar-Meléndez et al. [20] suggested that *C. annuum* was probably domesticated independently several times in different parts of Mexico from local wild peppers. They considered that independent domestications were more likely in chile pepper than in many crops because chile pepper, although a near-universal condiment in Mexico, is not a staple source of dietary calories, so yield was unlikely to be a primary consideration for those cultivating and eventually domesticating peppers. If traits of the domestication syndrome have indeed developed independently in different lineages of domesticated *C. annuum*, this may become apparent following comparative sequencing of genes controlling these traits.

Domestication and Diversification in *C. annuum*

Domestication is usually understood to involve heritable changes in the phenotype, and thus genotype, of a species in response to selection in the environment of cultivation. These changes often make the domesticate less fit for, or even incapable of, survival in the wild. The morphological traits affected constitute the domestication syndrome and frequently develop without conscious human selection. Diversification, on the other hand, often does involve conscious human selection. It usually occurs after domestication and may result in distinct variants within the crop, adapted to different uses. In chile peppers, domestication and diversification both affect primarily fruit characters.

The domestication syndrome includes increase in fruit size, change in fruit position from upright to pendent (hence fruits hidden amongst the foliage), and change from deciduous fruits that separate easily from their stalks when ripe to non-deciduous fruits that remain firmly attached even when fully ripe. These changes render the fruits less capable of being dispersed by birds. However, the first change to evolve may have been one that is not apparent morphologically. González-Jara et al. [18] found that the only obvious trait distinguishing cultivated from wild populations of *chile piquín* was increased rate of germination in the cultivated populations. Their local informants stated that slow and erratic germination of seeds from wild plants was a major barrier to their cultivation. Cultivation therefore imposes strong selection for rapid germination, although this is not conscious selection by humans. Similar selection presumably operated also in the earlier domestication(s) of Mexican chiles, since loss of seed dormancy is the only trait of the domestication syndrome that is fixed in all landraces and cultivars.

With regard to other traits of the domestication syndrome, variation in domesticated and wild peppers often overlaps. Fruits may be only 2 cm long in the smallest *serrano* peppers; the upright position persists in some variants of *serrano*, *mirasol* and other chiles; and some accessions of *serrano* have retained deciduous fruits, probably because *serrano* peppers are usually used while the fruit is still green, before it is attractive to birds, so there is no strong selection for loss of dispersal. In

C. annuum as whole, one therefore finds the whole spectrum from incipient domestication, represented by cultivated *chile piquín*, through various stages of semi-domestication, represented by the different combinations of wild and domesticated traits in *chile serrano*, to full domestication, represented by large-fruited chiles such as *ancho* and the non-pungent bell peppers.

Nothing seems to be known about genetic control of loss of seed dormancy in *Capsicum*, but multiple loci are probably involved. Understanding of the genetic control of other traits of the domestication syndrome in *Capsicum* lags behind, but has benefited from, studies in tomato. Fruit size is controlled by various quantitative trait loci (QTL), seven of which appear to correspond to similar loci in tomato, though the relative sizes of their effects in *Capsicum* differ from those in tomato and their modes of action are unknown [22]. Large fruits in domesticated peppers presumably result from "stacking" favourable alleles at a number of independent QTL, as in tomato. Some at least of these QTL appear to exert a general effect on other organs of the plant, because large-fruited peppers characteristically have larger leaves, larger flowers and flower parts, and larger seeds than wild peppers. Increased size of seeds has therefore been used as a criterion for recognising domestication in archaeological specimens of *Capsicum*, since seeds survive more often than intact fruits.

As in tomato, increased fruit size, particularly increased width, results in part from increased number of carpels. Nine QTL affecting this trait have been identified, one apparently corresponding to a similar locus in tomato [23]. Increasing the number of carpels appears to upset the mechanism regulating the number of parts in other floral whorls, because peppers with more than two carpels per flower usually have more than five sepals, petals and stamens.

Erect fruits are recessive to pendent and controlled by a single gene [24], though position is also influenced by other factors, notably weight of the fruits. Fruit dispersibility is also usually treated as a two-state qualitative character controlled by a single gene, with the deciduous trait dominant to non-deciduous [24]. The locus encoding a fruit-specific enzyme that causes softening of cell walls has been suggested as a candidate gene for this trait, in part because a cultivar of bell pepper was shown to carry a deletion in this gene that was absent in deciduous-fruited wild *C. frutescens* [25]. However, there is also a quantitative element to fruit dispersibility, since the strength of the tug needed to remove a fruit from the parent plant varies. Several anatomical features additional to softening of cell walls are probably involved in fruit abscission [26], so modifying genes as well as a single major gene are likely to be involved in loss of fruit dispersal in *Capsicum*.

Diversification in cultivated peppers includes presence, absence or degree of pungency; variation in fruit shape; colour of both mature and immature fruit; and differences in thickness and moisture content of the pericarp at fruit maturity. The latter determine whether the fruit is used fresh or dried. Most of these changes have probably resulted from conscious human selection of variants observed in cultivated populations, so probably arose post-domestication. A few plants in a home garden usually produce sufficient fruit for the household's needs. Households are likely to save their own seed and, since *C. annuum* is self-compatible, most of this seed will result from self-pollination or pollination from flower to flower on the same plant, so the resulting plants will be inbred to a considerable extent. Genotypes homozygous for recessive alleles will therefore segregate in the progeny of plants carrying recessive mutations. The new phenotypes are likely to be noticed and, if of interest, will be selected as seed parents. Those of their progeny that result from self-pollination will breed true for the recessive trait. Many of the variants associated with diversification in domesticated peppers are controlled by single genes, with the wild-type phenotype dominant, as would be expected under this scenario.

One exception is fruit shape, which is a quantitative character controlled by two or three QTL with major effects [22, 27]. Unlike tomato, in which fruit shape is determined before the flowers open, fruit shape in pepper is determined mainly after the flowers have been fertilised [28]. Fruit shape in pepper thus seems to be determined mainly by different QTL from those governing fruit shape in tomato [22]. Thickness of pericarp and cuticle, and moisture content of the pericarp at fruit maturity, are also quantitative characters and, as such, likely to be controlled by QTL but seem not to have been studied genetically.

Presence versus absence of pungency is a qualitative character, but degree of pungency is a quantitative character controlled by QTL on at least three different chromosomes [29, 30]. Pungency is due to a group of compounds unique to *Capsicum* known as capsaicinoids. They are synthesised in the epidermal cells of the placenta and accumulate beneath the cuticle, which may crack, so that capsaicinoids spread over the seeds and inner wall of the fruit [31]. This has led to the widespread, but incorrect, belief that pungent peppers have pungent fruit walls and pungent seeds. Non-pungency is recessive to pungency and, in most accessions of *C. annuum*, is controlled by a single gene, now designated *Pun1*, which encodes an enzyme that is suggested to catalyse the final stage in capsaicinoid biosynthesis [32]. Loss of pungency in *C. annuum* is associated with a large deletion at the start of this gene that disrupts both transcription and translation [32]. In a non-pungent accession of *C. frutescens*, loss of pungency proved to be due to a smaller deletion in a different region of the gene, hence must have arisen independently of the large deletion in non-pungent *C. annuum* [33]. Non-pungency in *C. chinense* is due to a third allele of *Pun1*, which carries yet another deletion [34]. Phylogenetic analysis of sequences of *Pun1* suggested that all three alleles for non-pungency arose before diversification of the *C. annuum*–*C. chinense*–*C. frutescens* complex, hence before domestication of any of these peppers [33]. This fits with the finding that some other wild species of chile pepper are polymorphic for pungency versus non-pungency [15]. However, the only non-pungent *chile piquín* that has been studied produced a pungent-fruited F_1 when crossed with non-pungent bell pepper. Its loss of pungency must therefore involve mutation at some locus other than *Pun1* [17]. It would be interesting to survey more populations of *chile piquín* for polymorphism for pungency, especially populations isolated from possible gene flow from commercially cultivated bell peppers, to characterise this postulated second locus for pungency and to determine whether or not the *pun1* allele of bell peppers occurs in genuinely wild *chile piquín*.

These studies of non-pungency in the *C. annuum*–*C. chinense*–*C. frutescens* complex show that the technical advances that are making gene sequencing quicker and cheaper are providing a new tool for investigating the origins and spread of lineages with similar traits that may have arisen independently within a crop. Fruit colour in chile peppers offers opportunities for such investigations, though these have mostly yet to be realised. Thus, the difference between red and yellow fruits in *C. annuum* is controlled by a single gene that encodes the enzyme that catalyses the final step in synthesis of the red pigments. Independent studies in France and Israel, using non-pungent yellow-fruited *C. annuum*, showed that yellow fruit resulted from a deletion at the start of this gene so that there was no gene product and hence no red pigments [35, 36]. However, a Chinese *C. annuum* with pungent yellow fruits carried a deletion for a single nucleotide in the coding region of this gene that produced a premature stop codon, hence a truncated protein unable to catalyse synthesis of red pigments. This suggested that the mutation to yellow fruit occurred independently in pungent and non-pungent peppers [37]. It would be interesting to investigate this further in Mexican chiles with yellow fruits.

Genetic control of orange fruit is more complex. Phenotypically similar orange colours can be produced either by accumulation of orange beta-carotene or by a mixture of red and yellow pigments [38]. Orange can result from mutations in genes controlling different steps in pigment synthesis and/or regulation of expression of these genes, but these changes are not yet fully understood [37]. At least one orange-fruited cultivar, "Fogo", carries the same single nucleotide deletion in the gene controlling the final step in the synthesis of red pigments as the Chinese yellow-fruited *C. annuum* [37], but the significance of this relationship is not clear.

Brown fruits, as found in *chile pasilla* and *chile mulato*, result from a mixture of green chlorophyll and red carotenoid pigments in the mature fruit. This occurs in genotypes homozygous for the recessive allele *cl*, in which chlorophyll does not break down as the fruit ripens [24].

Various reasons may be suggested for human selection and perpetuation of different colours and shapes in pepper fruits. Some relate to use of the fruit. For example, brown-fruited chiles are preferred for the dark brown *mole* sauces that combine chiles and chocolate. There probably also was, and is, an aesthetic element: ornamental peppers have been valued for their brightly coloured fruits, and have been used in dried flower arrangements, though hazards to children from pungent fruits have limited these uses. Many years ago, Standley [39] reported that indigenous people in Guatemala "cherish a firm belief that it is best to plant seeds [of maize and beans] grown on the premises. Otherwise the plants would never be happy; they would become homesick, as it were, pine away and the crop would fail". If this applied also to chile peppers, it could give rise to local subtypes, such as have been described for *serrano*, *ancho* and *jalapeño* [4], displaying small differences in fruit shape or other features. These may have arisen through founder effect followed by genetic isolation, but may now serve as markers for different local adaptations. Fruit colour may also serve as a visible marker for invisible qualities of the fruit. For example, in *chile costeño* yellow fruits were preferred, although they made up less than 5 % of the field population, because they were said to have better flavour and aroma than the predominant red fruits [4]. This is what Boster [40] called selection for perceptual distinctiveness.

Archaeological Record of Chile Peppers in Mexico

Ideally the archaeological record should provide some evidence on where and in what order the various traits associated with domestication and diversification appeared, but unfortunately remains of chile peppers are at present too limited for this. As Bruce Smith [41] noted, most of our knowledge of the early history of the major Mexican crop plants comes from just three regions: the caves of the Tehuacán Valley, the Ocampo caves in Tamaulipas and Guilá Naquitz cave in Oaxaca. Chile peppers have been recovered from all three regions.

Most of the specimens from Tehuacán come from Coxcatlán cave, with a few from late levels of El Riego cave. Some areas of Coxcatlán cave have been much disturbed and direct dates on presumed early remains of maize, beans and a cotton boll have shown all to be significantly younger than previously thought. None of the specimens of *Capsicum* has been directly dated, so they should be interpreted cautiously, particularly the large fragment of fruit, said to be indistinguishable from modern chiles in the local market. This fragment was stated by Earle Smith in the text of his report to come from Zone XI (Coxcatlán Phase, approximately 7700–5800 BP), but the caption of the photograph of this specimen assigned it to Zone II (Venta Salada Phase, about 1200 BP—Spanish Conquest) [42]. This fragment seems to have been the basis for the much-repeated claim that *C. annuum* "was certainly domesticated by the Coxcatlán Phase … and … [probably] planted from early El Riego times [approximately 8500–7700 BP]" [43]. When the Tehuacán project ended, the materials recovered, including the "ecofacts", were divided, with most remaining in Mexico but some going to the Peabody Foundation in the United States [44]. In 1971 I studied those specimens of *Capsicum* held at the Departamento de Prehistoria, Instituto Nacional de Antropología e Historia, through the courtesy of the Head of the Palaeobotanical Laboratory. I saw no fruit fragment of a size corresponding to domesticated pepper in specimens from the Coxcatlán Phase, but a single small deciduous fruit from this phase was very similar to modern wild *C. annuum*. The much later Palo Blanco Phase (about 2200–1300 BP) included a 19 × 14 mm fruit fragment that, from its size, represents a domesticated pepper. Most of the other specimens that I saw were seeds. Figure 17.1 shows the ranges in widths of seeds from different phases of the excavations compared to modern wild and domesticated *C. annuum*. Although the sample sizes are small, there is no discernible consistent increase in size through the various preceramic phases, from the earliest (El Riego, approximately 8500–7700 BP) to the latest (Abejas, about 5800–4600 BP). No chile specimens were recovered between the Abejas and Santa Maria Phases [42]. The Santa Maria Phase (about 3000–2200 BP) is the first to contain seeds of a size that must have come from a domesticated pepper.

I have also been able to examine some of the seeds from the Tehuacán coprolites, courtesy of the late Dr. E.O. Callen. Callen found that the chemical used to reconstitute dried coprolites and the material contained therein did not affect seed size [45]. He found a single seed of *Capsicum* in a coprolite from the El Riego Phase. This seed has a width of 3.3 mm, which is outside the range of modern wild *C.*

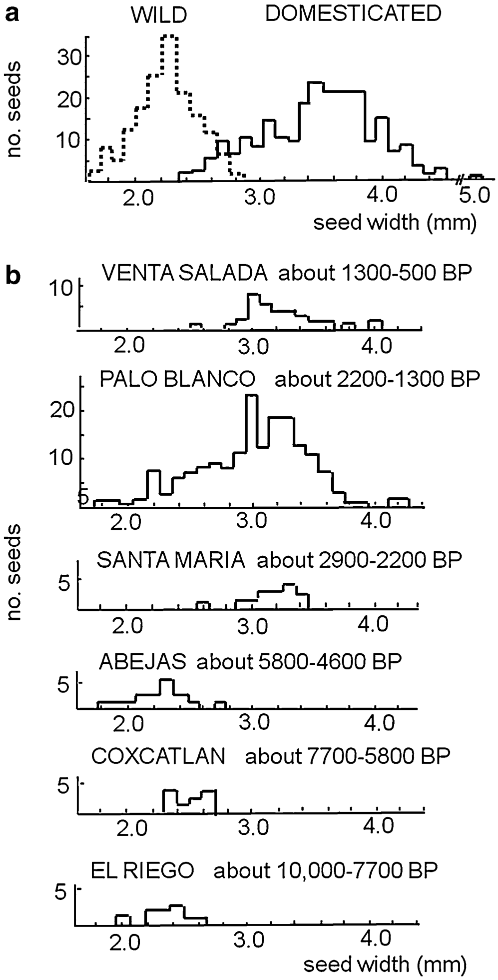

Fig. 17.1 Seed size in modern *Capsicum annuum* and archaeological *Capsicum* from Tehuacán. (**a**) Seed width in modern *Capsicum annuum.* (**b**) Seed width in *Capsicum* from Tehuacán

annuum, but also outside the range of any of the pepper seeds in the macrobotanical remains from any of the preceramic levels (Fig. 17.1). I therefore do not accept either this seed or the reported large fruit fragment from the Coxcatlán Phase as evidence that domesticated pepper was present in the Tehuacán valley in preceramic times. The earliest convincing evidence of domesticated peppers in Tehuacán comes from Santa Maria levels, after a long gap in the record of *Capsicum.*

Chile pepper was also reported from coprolites from very early levels of the Ocampo caves in Tamaulipas (Infiernillo Phase, about 9000–7000 BP). I found that these seeds have widths ranging from only 1.2 to 1.6 mm, so are smaller than any modern wild *C. annuum*. I therefore doubt whether they are in fact *Capsicum*, though they may be from another member of the Solanaceae with edible fruit, such as

Physalis. Similar small seeds were present in coprolites from the succeeding Ocampo Phase (about 6000–5200 BP), though in this phase they were accompanied by some larger seeds, most of which fall within the zone of overlap in seed size between modern wild and domesticated *C. annuum*. A semi-domesticated chile pepper, probably still with small fruit, may therefore have been present in Tamaulipas by 5200 BP.

Apart from two 8000-year-old specimens tentatively identified as "chilli stems" [46], all the specimens from Oaxaca are much more recent, about 1400–1000 BP. They have been described in detail by Perry and Flannery [46] and I have also been able to examine them. Most are fruit stalks, but there are some incomplete fruits, fragments of fruit wall, and seeds. Perry and Flannery [46] concluded that the specimens were from domesticated peppers, because the fruits were non-deciduous (when it was possible to determine this), larger than those of wild peppers, and the seeds were of a size indicating domestication. The distinction between deciduous and non-deciduous fruits as a criterion of domestication may not be easy to apply to archaeological material, because immature fruits remain firmly attached to their stalk regardless of whether the ripe fruit is deciduous or non-deciduous. Immature fruits are likely to have been used prehistorically because they are pungent but not taken by birds. Fruit and seed size are less equivocal indicators of domestication, and I agree with Perry and Flannery [46] that their specimens came from domesticated peppers, although widths of seeds and fruit stalks are all within the lower part of the range of modern domesticated *C. annuum* (Fig. 17.2), indicating that fruit size has increased considerably in the last 1500–1000 years.

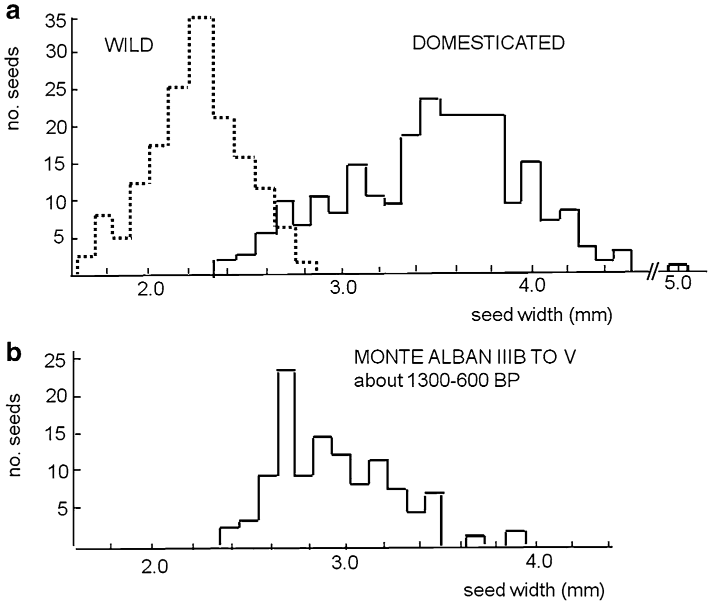

Fig. 17.2 Seed size and width of fruit stalks in modern *Capsicum annuum* and archaeological *Capsicum* from Guilá Naquitz. Lines below (**c**) represent ranges in individual accessions of modern peppers. (**a**) Seed width in modern *Capsicum annuum*. (**b**) Seed width in *Capsicum* from Guilá Naquitz. (**c**) Width of fruit stalk in modern *Capsicum annuum*. (**d**) Width of fruit stalk in *Capsicum* from Guilá Naquitz

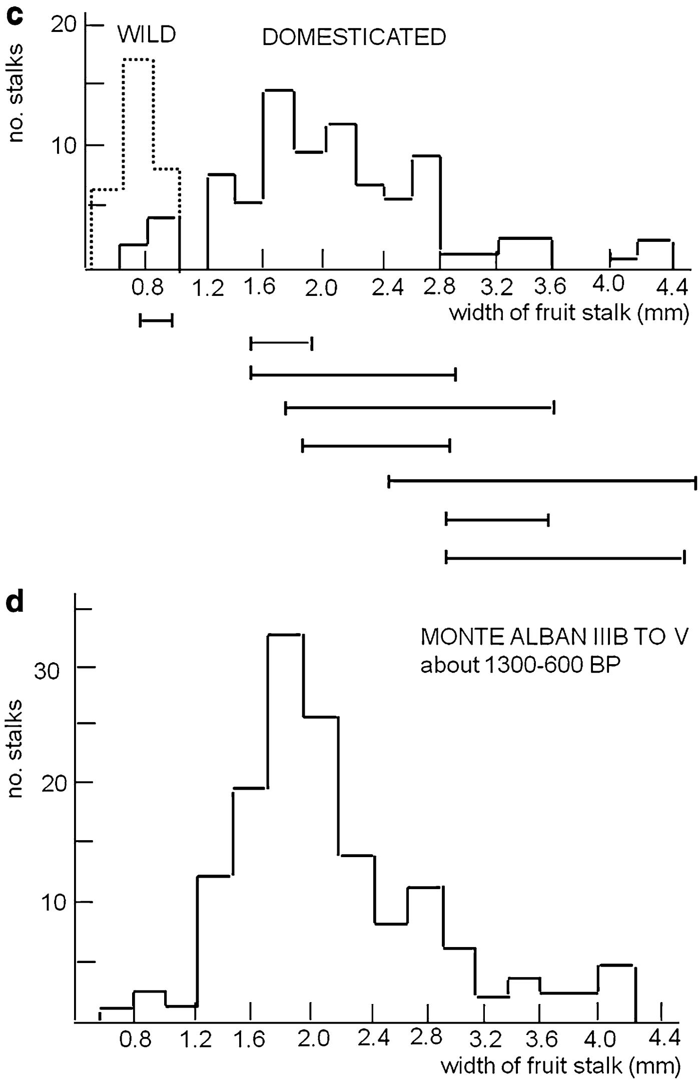

Fig. 17.2 (continued)

Perry and Flannery [46] considered that ten different types of domesticated pepper were present in their sample, and suggested that some were used fresh and some dried. My study suggested that one type had relatively small fruits, borne on slender stalks and with the base of the calyx clasping the fruit, which was therefore probably elongated in shape. Another type had much stouter fruit stalks, indicating that the fruits were larger and heavier than the first type. These stalks were often curved, indicating that the fruits were pendent. Some fruit stalks had widely flaring calyces, suggesting that the fruits were more spherical than the elongate fruits enclosed by clasping calyces. Values for widths of seeds or fruit stalks showed that specimens from the same square of the excavation sometimes varied more than any single modern type. This may indicate that several different types of pepper were stored, used or discarded together, or may simply mean that 1000 years ago farmers were less careful about rogueing their crop or selecting their seed to keep the crop homogeneous. Landraces of chile pepper still display considerable heterogeneity [4, 47], so although I agree that different types of chile pepper are represented among the Oaxaca specimens, indicating that some diversification had occurred, I am not convinced that as many as ten different types were present.

Carbonised chile seeds were recovered from rubbish in subterranean storage chambers dated about 5000–4250 BP, and also numerous specimens of chile from a much later house site, at Teotihuacán [1], but I have not seen these and they do not seem to have been described in detail.

The archaeological record of *Capsicum* therefore currently suffers from a significant gap in time spanning the period when domestication, and probably initial diversification, took place. Despite frequent statements in the literature, there is no convincing evidence that chile pepper was among the first species domesticated in Mexico. On the contrary, human selection pressures were probably relatively weak during the first millennia of utilisation by humans, so domestication would occur only slowly. Since green fruits are pungent, hence attractive as a spice, there was probably no strong early selection for loss of dispersal. Yield is unlikely to have been a primary consideration in a species grown to provide flavouring rather than for dietary calories, so there is unlikely to have been strong selection for larger fruits, as witnessed by the slow increase in size of seeds from various levels of the Tehuacán excavations. Various semi-domesticated peppers with different combinations of wild and domesticated traits still exist today, demonstrating that domestication of cultivated *C. annuum* is still not complete.

Chile Peppers in Mexico at the Time of the Spanish Conquest

The records of the tributes paid to the Aztecs at the time of the Conquest, and to the Spanish crown after the Conquest, show that impressive quantities of chile must have been grown. Texcoco paid annually 18,250 large baskets, comprising fruits sorted into three different sizes, while three towns in what is now San Luis Potosí supplied 1600 carrier-loads of dried chile per year, one load for a professional carrier being 50 kilos [1]. Chile was more than just a condiment, as shown by the descriptions of Sahagún quoted at the start of this chapter. Different types of chile contributed different flavours and degrees of pungency to dishes that often required complex blending of their ingredients. For example, 12 different types of chile could be used in preparation of *mole poblano* [4].

Chiles also had various medicinal uses [1]. A slight cough was treated with a gruel made of yellow chile and honey; a more persistent cough with lime water mixed with chile. Earache was treated with chile, alone or mixed with resin of *Bomarea hirtela*. Seed of *Geranium carolinianum* mixed with chile and salt was recommended to prevent scale forming on teeth, while a mixture of hot chile and salt alleviated toothache. Chile was also included in remedies for blood in the saliva. This can be a symptom of scurvy, and chiles are an excellent source of vitamin C, which is an effective anti-scorbutic. For stomach ache, Sahagún recommended drinking juice of yellow tomato mixed with chile. Colic was treated with a suppository made from lime, saltpetre, drops of liquidambar sap and chile. As Long-Solis [1] remarked, this remedy would cause a pain more intense than the original one.

The *Codex Mendocino* shows the use of chile as punishment: a father is depicted holding his 11-year-old son in the smoke of a fire on which dried chiles have been thrown, while a mother threatens her 6-year-old daughter with the same punishment [1]. This punishment still occurs among the Popoloca of Veracruz and Puebla [4]. Outside Mexico, chiles have even been used in chemical warfare: the fort built by Columbus on Santa Domingo was attacked by indigenous people lobbing calabashes of wood ashes and ground chiles into the fort [2].

The importance of chile in Mexico at the time of the Spanish Conquest is shown by the fact that chile had its own goddess, a daughter of Tlaloc, the rain god, who was one of the most important gods in the Aztec pantheon [1].

Chile Peppers in Present-Day Mexico

Most Mexican chiles can be distinguished by whether they are used fresh or dried. Those used fresh include sweet peppers and the pungent *jalapeño* and *serrano*. Those used dried include *mirasol* and *pasilla. Chile ancho* and similar types are sold either fresh or dried, depending in part on the prices prevailing at the time of harvest.

Sweet peppers are grown primarily for export. Production is centred in the northern state of Sinaloa, close to the main markets in the United States. The principal cultivars are those familiar in the United States, such as ‘California Wonder’ and ‘Yolo Wonder’.

Jalapeño is probably the best known pungent chile outside Mexico. The cuticle of the fruit develops distinctive corky cracks while the fruit is still green, and these persist in the mature fruit. Fruits with 30–60 % corkiness are preferred for pickling, because this prevents separation of the cuticle during pickling. Fruits with more corkiness are ideal for drying by smoking to produce *chipotle*. This practice goes back to pre-Conquest times and may have been used to preserve chiles from one harvest to the next [1, 4]. In 1978, a single pizza franchise in the United States used almost $2 million worth of hot chiles, mostly *jalapeño* [10]. This has led to breeding of cultivars of *jalapeño* to suit North American tastes. Some of these are grown in Mexico for export to North America, but are considered by Mexicans to lack the characteristic *jalapeño* flavour, so to be unacceptable [4].

Serrano is a widely grown and variable pungent chile. In 1974 an improved cultivar, ‘Tampiqueño-74’, bred in Mexico, was released and within 12 years accounted for about half the production of *serrano* in Mexico [1], raising concerns about erosion of genetic diversity. A similar situation may be occurring in the large-fruited dual purpose *ancho* chiles. Hybrid cultivars have been developed for the fresh market, and are preferred because they are more uniform in size, shape, colour, texture and flavour than the landraces that they are superseding [1]. However, the market for dried *ancho* is still supplied by heterogeneous landraces [47]. Names in the *ancho* group are confusing. Laborde and Pozo [4] used *ancho* to include both fresh and dried chiles, while Long-Solís [1] used *chile poblano* for types used fresh, *ancho* for dried types with red fruits and *mulato* for dried types with brown fruits.

There is a similar profusion of names for other chiles. *Pasilla* has long, relatively mild fruits that ripen brown and are mostly used dried for *salsas* and *moles*, but a small quantity is used fresh and then called *chilaca* [4]. *Mirasol* is a variable group of pungent chiles, used green on a small scale when *serrano* is not available and known as *guajillo* or *cascabel* when dried. The latter name comes from the rattling of seeds within the dried fruit. A comprehensive dictionary of common names and identifications of the different Mexican chiles is given by Long-Solís [1].

Concern about genetic erosion in Mexican chiles has led, on the one hand, to collecting and ex situ conservation in Mexico for use in national breeding programmes, and on the other hand, to studies of the amounts and distribution of genetic diversity within and between populations of chiles of different types. Such studies provide essential background for any programme of in situ conservation. An early study, using variation in isozymes, found greater variation in wild than domesticated *C. annuum* [21]. Accessions collected from family gardens had the least diversity, which the investigators suggested was probably because many were descended from a single plant, imposing a severe genetic bottleneck. Individual wild populations consisted mostly of similar genotypes, so variation was mostly between populations. On the other hand, another study [19], also using isozymes, based on more plants per population but fewer populations, and restricted to northwest Mexico, found similar levels of genetic variation in ten wild and three domesticated populations (one each of *serrano*, *jalapeño* and bell pepper). In both wild and domesticated populations, most of the observed genetic variation occurred within populations, but there was more genetic differentiation among the three domesticated populations than among the wild populations, suggesting that domestication had partitioned genetic variation between different types of chile. A similar study of populations from northwest Mexico using DNA polymorphisms (RAPDs) detected more diversity but confirmed that there was more genetic differentiation among the domesticated than the wild populations, possibly due to different directions of human selection among the domesticated chiles, but possibly also because only three domesticated populations, representing very different types of chile, were sampled. A fourth study, again confined to northwest Mexico but using microsatellites and a greater number of domesticated populations, including landraces and hybrid cultivars, found considerable genetic differentiation among populations at all three levels (wild, landrace, hybrid cultivar) but most genetic variation occurred within rather than between populations [48]. Since significant genetic variation is apparently maintained both within and among populations, collections for ex situ conservation should sample a significant number of individuals per population, as well as a significant number of populations.

Concerns similar to those expressed for *Capsicum* about erosion of diversity in traditional landraces following introduction of improved hybrid cultivars and their adoption by farmers have also been raised for maize, but shown to be less serious than originally feared. Although maize farmers trialled, and often adopted and adapted, new cultivars, they continued to maintain their traditional landraces because they offered security in adverse conditions [49, 50]. Similar studies are needed on farmers' practices and their effects in relation to on-farm conservation of genetic resources of chile peppers.

Epilogue

Columbus raised money for his first voyage by promising Ferdinand and Isabella of Spain that he would bring back, among other things, rhubarb and spices. He never found any rhubarb, but in the West Indies encountered both allspice and chile pepper. In the journal of his first voyage he recorded that "there is much *axi*, which is their pepper, and it is stronger than pepper, and the people will not eat without it". This was probably *C. chinense*, which is still widely grown in the Caribbean. Columbus brought chile seeds back to Europe, where the plants were initially grown in greenhouses [51], which also suggests that it was *C. chinense* rather than the more cold-tolerant *C. annuum*. However, after discovery and conquest of the Mesoamerican mainland, Spanish missionaries sent back to Europe seeds of various species used in this new land, for trial in monastery gardens. Among these would almost certainly have been *C. annuum*.

Like other New World Solanaceae, such as tomato and potato, chile peppers initially received some bad publicity, presumably because they were recognised as related to such poisonous European species as deadly nightshade, mandrake and henbane. Around 1570 Matthiolus claimed that chiles caused disease of the kidneys and liver [51], while in 1595 Dodonaeus wrote that it was dangerous to eat chile if one was bled often and "it killeth dogs" [10]. However, these warnings were offset by Europeans returning from the New World accustomed to food seasoned with chile. Consumption of chile spread rapidly, particularly in Portugal, perhaps because it could be grown locally, hence was much cheaper than the imported and expensive black pepper. Portuguese spice merchants, faced with losing a lucrative monopoly, organised prohibition of cultivation of *Capsicum* and destruction of the plants [51, 52]. Chiles also entered Europe through the back door, as it were, having been acquired by the Turks and spread to the Balkan peninsula, notably Bulgaria and Hungary, with the expansion of the Ottoman Empire [1]. In Hungary, *Capsicum* was initially known as Turkish pepper, while maize, introduced by the same route, was called Turkish wheat and the English name of the turkey perpetuates this role of the Turks in spreading products of the New World to Europe [1].

By the seventeenth century, sailors customarily carried dried chiles on transatlantic, and presumably other, voyages. Three sorts of chile were known in India by 1542 [53] and spread from there back to Germany, which misled the herbalist Leonhard Fuchs into thinking that *Capsicum* was native to India [10]; a belief still shared by many inhabitants of the subcontinent, who find it hard to believe that, prior to the early sixteenth century, curries and other local dishes owed their pungency to spices other than *Capsicum*. The Spanish and Portuguese are credited with spreading chile peppers along their trade routes to the Indian subcontinent and the Far East. The current global dominance of Mexican domesticated *C. annuum* is thus due in part to historical accident, but probably in greater part to the adaptability that has enabled *C. annuum* to be successfully cultivated in so many different continents and climates.

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Chapter 18
Cotton: Traditional and Modern Uses

Ana Wegier, Valeria Alavez, and Daniel Piñero

Abstract Cotton, *Gossypium hirsutum* L., is one of the most important crops for humanity. It is placed among the top ten most widely grown crops in the world even though its main purpose is not food. In addition to the appreciation for its fibers, cultures learned to use the whole plant for many uses, from controlling reproduction and pharmaceuticals to pigments and cattle feed.

Wild populations of this species, that inhabit coastal dunes and lowlands, are heavily impacted by multiple factors that limit their proper conservation, such as land use changes caused by the development of resorts, roads, residential areas, and the general disturbance of coastal areas. On the other hand, biosecurity measures currently taken have proved inefficient in the face of gene and transgene flow with cultivated relatives of the same species.

In 2002, we began to study the populations of wild cotton to propose strategies that could contribute to in situ conservation of the species in Mexico, its center of origin and diversity. Since then, we have made multiple visits to each of the cotton metapopulations and talked to the people living in the same communities. We also investigated the genetic diversity, interactions between plants and insects, bacteria and fungi while documenting uses and traditions preserved by the people, which became valuable contributions that motivated us to write this chapter. We noted that the problems caused by migration, poverty, and loss of consciousness by the younger generations transcend from cotton conservation to society as a whole. These situations pointed out that long-term conservation of plant genetic resources of Mesoamerica will only be possible through the preservation of ancient knowledge about the care of crop fields (such as milpa), traditional and medicinal uses of plants, indigenous languages, gastronomy and general habits and customs that shaped the great biodiversity of Mesoamerica to domesticate over 150 crops that are important to humanity today.

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Thus, one way to create conservation strategies for these plants is to make information available to all public about their past, present, and potential uses in order to promote care for the plants and their environment at local and global levels. In this chapter, we will discuss traditional and current uses of *G. hirsutum*, especially in Mesoamerica, because this region is its center of domestication and therefore, where the longest relationship with human civilizations has been established. Here, we show that instead of taking advantage from their great potential for generating long-term biosafety conditions and improving conservation strategies for this species at its center of origin and diversity, our society is wasting opportunities of the multiple uses cotton could provide.

Keywords Cotton • In situ conservation • Genetic diversity • Traditional uses

Introduction

Cotton has been a fundamental natural resource since the origin of various civilizations and today remains as one of the groups of species most important plant species for mankind [1, 2]. It is the most widely used natural fiber and the sixth largest source of vegetable oil [3]. Also, ranked seventh in the world cultivated area and genetically modified cotton is the third most planted biotech crop worldwide [3, 4]. It is important to note that within the fifteen most important crops, cotton is the only one that did not acquire its value by being a staple food [2].

Given its economic importance worldwide, Cotton (*Gossypium* L.) is a genus that has captured the attention of agricultural scientists, taxonomists, and evolutionary biologists. Especially in recent decades, molecular technologies have been implemented to answer questions about the origin of polyploidy species, the phylogenetic relationships inside the genus and the origins of domesticated plants from their wild progenitors, among others [2].

Perhaps the most striking aspect of cotton domestication is that given the wide geographical distribution of the genus, different species became involved with ancient cultures in different continents, which led to a process of convergent or parallel domestication from divergent and geographically isolated wild ancestors. This parallel domestication involved four species: two American, *G. hirsutum* and *G. barbadense*, and two African and Asian, *G. arboreum* and *G. herbaceum*. Thousands of years ago, the inhabitants of different regions of the world discovered, independently, the unique properties of the fibers of these four cotton species and began to select them for manufacturing thread, ropes, textiles, and other applications. Each of these species has a unique history of domestication, diversification, and use [1] that has modeled their genetic structure through management and artificial selection of the variation caused by evolutionary processes over millions of years.

Of the four domesticated species of cotton, *Gossypium hirsutum* L. represents 95 % of the current production and most wild populations of this species live in Mexico. Although there has been extensive research on its biology, ecology, and genetics, most have been performed on domesticated plants and outside its natural distribution range; therefore, little is known about the whole species since, after the domestication process, only part of the variation that could be found in wild populations is preserved in other areas. Consequently, research on domesticated plants should be used with caution and without extrapolating to the rest of the species.

The* Gossypium *Genus

Gossypium seem to have diverged from its closest relatives during the Miocene, subsequently expanding worldwide by various transoceanic dispersal events, acquiring its current geographical distribution [5]. The taxonomy of the genus has been well studied. The species are grouped into four subgenera (i.e., *Gossypium* L., *Houzingenia* Fryxell, *Sturtia* R. Brown Todaro, and *Karpas* Rafinesque) and seven sections. This classification system is based primarily on morphological and geographical evidence, although most infrageneric classifications are consistent with cytogenetic and molecular data [2]. The centers of diversity of the genus are defined by being rich in number of species and include Australia, the Horn of Africa (Somalia, Djibouti, Eritrea, and Ethiopia), the southern Arabian Peninsula, and the western part of central and southern Mexico [1, 2, 6, 7].

Currently, the extraordinarily diverse genus *Gossypium* includes about 50 species [2]. As the genus diversified and expanded, an extensive chromosomal evolution followed. Although all diploid species share the same number of chromosomes ($n=13$), DNA per genome is very variable. Chromosome morphology is similar between closely related species, and this is reflected by the ability of species to produce hybrids that display regular pairing of chromosomes during meiosis and sometimes high fertility in F1. In contrast, crosses between more distant relatives are difficult to make and those that are successful often have abnormalities during meiosis. The collective observations of mating behavior, size of chromosomes, and the relative fertility in interspecific hybrids led to the designation of single letter symbols to define groups of species sharing each genome type. Currently, eight sets of diploid genomes are recognized (i.e., from A to G and K; [5]).

All *Gossypium* species produce seeds with elongated epidermal cells that resemble short cylindrical hairs (1–3 mm); however, the species from which the cultivated cottons were domesticated present a second layer of longer hairs (10–25 mm), with thinner secondary cell walls possessing cellulose strands that laid down in periodically reversing spirals [2, 8]. These kind of longer fibers can be spun into a yarn because when they desiccate at maturity form a flattened ribbon that lastly convolutes and twists because of the structure of its cell walls (Fig. 18.1) [2, 7]. The layer of elongated lint, the main target trait selected for domestication, is restricted to the A (African–Asian) and AD-genome (American) species of *Gossypium* [2].

Fig. 18.1 Cotton fiber. *Up*: Lateral view of cotton mature bolls with fiber exposed, from wild (*left*) to domesticate (*right*). *Center*: Upper view of cotton mature bolls, from wild (*left*) to domesticate (*right*). *Down*: transformation of cotton bolls into yarn and thread (from *left* to *right*)

Origin and Distribution of Diploid Domesticates

The cultivated A-genome diploids of the Old World, *G. arboreum* and *G. herbaceum,* are known primarily as crop plants, but the time and place of its domestication remains unclear. These short-staple cottons (fiber length <23 mm) are important regionally (i.e., Africa and Asia), while allotetraploid cultivates still dominate cotton production in the world [2, 9].

Gossypium herbaceum subsp. *africanum* is regarded as the wild progenitor of cultivated *G. herbaceum* subsp. *herbaceum* given its distinct morphology and that it is fully established in southern African forests and grasslands, which are generally accepted as the source of the original *G. herbaceum* cultigens although today this region is far away from historical or present diploid cotton cultivation [2, 9].

On the other hand, no wild progenitor is known to *G. arboreum*. The Indus Valley (Mohenjo-Daro) could be regarded as its possible center of original domestication because it is the center of diversity for this species; however, centers of diversity do not necessarily correspond to original geographic points of origin [2]. In fact, Hutchinson [10] considers the Indus Valley cottons to be more similar to northern, more agronomically advanced *G. arboreum* cultivars [2]. *Gossypium arboreum* has five races: (a) *Indicum*, (b) *Burmanicum*, (c) *Sinense*, (d) *Sudanense*, and (e) *Cernum* [9]. Race *Indicum,* a primitive perennial domesticate, represents the most agronomically primitive form of *G. arboreum,* which was subsequently dispersed into peninsular India and along the east coast of Africa and perhaps into East Asia as a consequence of the Indian Ocean trade routes and with the rise of modern textile industry [2].

The only archeological remains (i.e., cloth fragments and yarn) from diploid domesticates were recovered in India and Pakistan (dated to 4300 years B.P.) and belong to *G. arboreum.* No archeological evidence about *G. herbaceum* has been identified but its wide distribution prior to the development of industrial textile manufacturing imply a history of domestication at least as long as that of *G. arboreum* [2].

Origin and Distribution of Allotetraploid Domesticates

The allotetraploid cottons are the result of the union of two genomes, A and D, which evolved in different hemispheres and diverged isolated from each other for millions of years [2].

Long-distance dispersal played an important role not only in the diversification of major lineages but also in speciation within genomic groups of *Gossypium* [2]. Multiple intercontinental dispersal and transoceanic pathways are inferred during the evolutionary history of the genus. These include, at least, one dispersal event between Australia and Africa, another to America (probably Mexico) leading to the evolution of diploid D genome and a second, much later, colonization of the New World of the genome A ancestor that gave rise to the allopolyploid genome AD. Wendel and Albert [11] raised the possibility of a radiation prior to the domestication of the A-genome in Asia, followed by a transpacific migration, rather than a transatlantic one. This possibility is supported by the biogeography of D-genome species, following the hypothesis that they originated in western Mexico [2].

The origin of American *Gossypium* allopolyploids remained a classic mystery of botany for half a century. Today, genetic sequence data convincingly demonstrate that allopolyploids originated in the Middle Pleistocene, between one and two million years before the earliest records of *Homo sapiens*, therefore, making unlikely that *Homo sapiens* could intervene in the process of hybridization. A-genome species (i.e., *G. arboreum* and *G. herbaceum*) are equally divergent from the A-genome of allopolyploids. The identity of the donor remains unclear although it seems to be most closely related to the present-day *G. herbaceum* because at the genomic level, both A-genome diploids differ from A-genome allotetraploids by reciprocal translocations of chromosome arms, but *G. herbaceum* presents two translocations instead of three like *G. arboreum* [12–14].

The closest living relative of the D-genome parental donor is *G. gossypioides* [2, 15, 16], although, historically, there has been another candidate: *G. raimondii* [17]. However, DNA sequence data revealed extensive recombination and introgression with rDNA sequences from A-genome cottons which could be explained by an ancient hybridization event, between *G. gossypioides* and an A-genome species [2]. Another aspect of the history of polyploid cottons that has been clarified is that all possess the A-genome cytoplasm and, most likely, from a single source. Studies employing nuclear genes (inherited biparentally) lead to the same conclusion. Thus, evidence indicates that all allopolyploid cottons come from the same ancestors [2].

Considering a Pleistocene origin of allopolyploid cotton species, it could be inferred that morphological diversification and expansion must have happened very quickly. Five allopolyploid species are recognized: *G. darwinii* is native to the Galapagos Islands, where it forms extensive and abundant populations in some areas. *G. tomentosum*, native to the Hawaiian Islands has a much more diffuse population structure, mostly as scattered small populations on several islands. A third allopolyploid, *G. mustelinum* is a rare species restricted to a relatively small region in northern Brazil [18]. *Gossypium barbadense*, meanwhile, presents a southern natural distribution, concentrated in the northern third of South America but with a broad overlapping area of with *G. hirsutum* in the Caribbean. Finally, *G. hirsutum* has a wide natural range, collectively presenting a morphological richness that covers the continuum of wild to domesticate. Wild *G. hirsutum* is distributed in the coastal dunes and tropical rainforests of Mesoamerica and has even been reported in remote Pacific islands like the Solomon Islands or the Marquesas. The latter two species were domesticated independently by Hispanic cultures [1].

Gossypium barbadense

The original domestication of *G. barbadense*, also known as Pima or Egyptian cotton, most probably occurred in South America, along the coastline of central Peru, where the earliest archeobotanical remains dated 5500 years BP were recovered (e.g., plant remains like seeds, fiber or fruits, or manufactured remnants of yarn, fishing lines, nets, and textiles) [2, 19]. The primitive agronomic characteristics of the remains along with molecular evidence that uncovered a center of genetic diversity in agreement with the geographic area where wild populations are distributed support this hypothesis [2, 7].

Today, *G. barbadense* is produced in several regions of Central Asia, Egypt, Sudan, India, the United States, and China. This species presents long, strong, fine fibers, but its yield is relatively low, specially compared to *G. hirsutum*, which is why it accounts for less than 10 % of total world cotton production [2].

Gossypium hirsutum

Gossypium hirsutum or “upland” cotton, accounts for more than the 90 % of the cotton production in the world, and its cultivars are widely distributed worldwide ranging from tropical to temperate latitudes in approximately 40 countries, being China, the United States, and India the main producers [3]. It is the only genetically modified species of *Gossypium*.

Gossypium hirsutum has a long history in Mesoamerica. This region is the center of origin and genetic diversity of wild populations, and it is the place where the relationship with human civilizations was first established [20]. Therefore, it is in Mesoamerica where upland cotton domestication took place, and this process meant the starting point of a relationship that developed into a deep cultural, economic, and anthropological association that prevails until today.

With the advent of novel technologies, extensive cultivation and the growth of international commerce, cotton applications have increased in diversity and have expanded worldwide. In the following pages we will review both, the traditional uses of *G. hirsutum* at its center of domestication and its modern uses.

Traditional Uses of *Gossypium hirsutum*

The oldest archeobotanical remains found at the Tehuacan Valley set cotton utilization and cultivation as early as 4000–5000 years BC [2], while ethnographic descriptions, historical records, and pictorial sources reveal that Mesoamerican civilizations—from Olmec to Maya and all Central Mexico cultures—were accomplished weavers and appreciated cotton and textiles among their most valuable resources, which had an important impact on social, political, and economic practices of Prehispanic times [21–24].

Spinning and Weaving: Technologies and Significance

Ethnohistorical evidence confirms that during Prehispanic Mesoamerica, cotton thread was spun by hand of women by means of, generally, three simple tools: (1) a thin wooden spindle fitted with (2) a ceramic disk or whorl, and (3) a small ceramic bowl used to support the spindle as it twirled. These instruments were commonly made with ceramic although wood, stone, and other materials have also been described [24].

Cotton textiles where clearly manufactured and used in Central Mexico from a very early date but with time, as the scale and intensity of cotton demand increased, more specialized spinning equipment developed and more people became involved in waving efforts [24]. Subtle differences in spinning techniques may have existed among cultures, for instance, Mixtec codices from Oaxaca do not depict the use of a support bowl, while practically all Central Mexico civilizations used it [24].

Spinning and weaving were activities that had a deep significance to the feminine identity and social status of Mesoamerican women, from their birth until their death. Aztec girls, for instance, were presented with weaving tools as a birth ritual and began to learn how to spin and weave at a very young age. Maya women were also skilled in these activities. On the other hand, Mesoamerican women were traditionally buried with their spinning and weaving equipment suggesting the importance of carrying these tools into the afterlife [22, 23]. Certain types of spinning and weaving such as spinning of elite fibers like cotton and the incorporation of precious materials (e.g., dyes, feathers, and pearls) into textiles were highly respected elite activities carried out by noblewomen whose tools were made of elite materials, including gold and much others [23]. However, spinning artifacts found near Xochicalco proved to be abundant and ubiquitous; a finding that suggest that both, elite and commoner women, participated in textile production [24].

Finally, Mesoamerican cultures possessed a profound devotion to their deities, which portrayed their most valuable ideologies about life. Weaving was associated with the Maya female goddesses Ix Chebel Yax, the "wife of the creator," and Ix Chel, the "Moon Goddess," and Aztec and Maya goddesses of childbirth were also the goddesses of spinning and weaving [22, 23].

Textiles

Textiles have traditionally played an important role for Mexican indigenous groups like the Aztec, Maya, Zapotec, and several other peoples of Mesoamerica from the Classic period (200 BC) to the present day.

In Prehispanic Mesoamerica, textiles were highly esteemed as commodities on a level similar to gold and jade and possessed a wide variety of uses and significances. The uses of textiles could be separated in four primary categories [21, 23, 24]:

1. *Clothing*: cotton garments were used as vestments especially for the elite, since cotton was the most esteemed fiber among the fiber producing plants (e.g., maguey or yucca). In the Basin of Mexico, cotton was an import, which implied that textiles could only be worned by high-status people. However, textiles varied in quality and not all were destined to high society clothing, but served instead for many common everyday activities such as covers for tortilla or wraps for the deceased.
2. *Armor manufacture*: textiles were an important element of armors or *ichcahuipilli*, which placed them as very valuable items since war was an important element to Central Mexico civilizations with significant ritual and religious implications and warriors were highly recognized members of society. Cotton

clothes were combined with woods and feathers to produce light, however strong, shields, and the essential body armors of Mesoamerican warriors.

3. *Sociopolitical significance*: In Mesoamerica, wearing, possessing, or manufacturing high-quality decorated textiles was a symbolic demonstration of power, wealth, or position which was an important element of elite exchange, politics, and status validation. Textiles could be used to signify geographic origin, status, and rank or conversely, its absence, especially clothing, was a widespread symbol of loss of status and degradation. Finally, textiles and textile production activities served as metaphors for several Mesoamerican deities.
4. *Economic commodity*: textiles were valuable commodities for exchange in the economic systems of the time, i.e., tribute and markets. Textiles played an important role transferring economic value over large distances in Prehispanic Mesoamerica because they were very valuable items that had very low weight and thus were very easily transported.

Commerce, Trade, and Tribute

Textiles formed a major part of ancient Mesoamerican economy. Cotton and textile-related transactions involved several levels according to the stages of the productive chain, from the raw material production and transportation to the spinning, weaving, and in certain cases embellishing; and finally, to the consumer. However, many distribution mechanisms and networks were required to accomplish the dynamism of cotton movements in Prehispanic Mesoamerica such as marketplace exchange, foreign trade, and tribute [21].

Dealing in cotton or in cotton cloth was an economic enterprise of a high order, which took place from the grand Tlatelolco marketplace, to sensitive borderland markets (e.g., Cholula), to small marketplaces within the Aztec empire and beyond. However, the spun thread, not woven, does not seem to have been a market or trade item [21].

Raw cotton fibers were extensively transported by local producers, local merchants, and long-distance merchants (i.e., *oztomeca*). Cotton cultivation requires a constant warm temperature (i.e., 61° to 77 °F or 16° to 25 °C) and a heavy rainy season. Such conditions were met in the wild distribution of *G. hirsutum*, and therefore was in these areas (Mexican Pacific and Gulf coastal areas) were Prehispanic civilizations could grow cotton. However, cotton could also grow at inland regions that possess warm temperatures and adequate water sources to maintain irrigation, usually at valleys below 1000 m in elevation (e.g., the State today known as Morelos). Given these restrictions, cotton could not be grown in Central Mexico highlands (e.g., Tenochtitlan) and therefore transportation and exchange of raw materials, most probably occurring at marketplaces, was essential to allow spinning and weaving activities in the areas where cotton cultivation was not viable [21].

Historic documents and codices indicate that textiles were used extensively for tribute in central Mexico. Tribute involved a payment in goods or services, or both, of conquered districts to Tenochtitlan. Cotton as a raw material was given in tribute by four provinces and all but two provinces, of 38, provided textiles as tribute. For instance, the Matricula de Tributos (Tribute Roll), a document listing the tribute paid by the various tributaries of the Aztec empire, pictorially illustrates 60,400 mantles, each to be rendered in tribute four times yearly, yielding a total annual tribute of 241,600 mantles. Cotton mantles were also a key form of tribute in colonial Yucatan; cloth also is portrayed as an offering in the Maya codices whereas the spinning of cotton constituted a tribute service for some towns in the Valley of Mexico [21, 22].

Finally, foreign trade involved the movement of elite textiles and was carried out directly by rulers of sovereign city-states themselves. This kind of high-level exchange between Mexica emissaries and foreign rulers across, sometimes, tense boundaries, had political and economic advantages since it strengthen or promoted the relations between city-states [21].

Maintaining Traditions Alive

An important part of cotton historical and current applications, from textile design, social and religious meanings, weaving techniques and tools, among others, is being rescued in Mexico by individual efforts, non-governmental organizations and public institutions. People who are working to preserve and document the history of textiles in their places of origin have become specialists on the subject and have achieved a collaborative network that brings together 350 weavers (from 12 to 70 years old) in all regions of Oaxaca involving nine indigenous communities, who have achieved to establish a production mechanism based on the preservation of techniques, processes, and traditional elements involved in textile manufacturing and strengthening the pride and admiration to those who perform this work in order to inherit it throughout the generations [25].

The network starts with communities that (1) collect wild cotton fibers, that are involved in production projects and participatory breeding (with the support of MS Flavio Aragón) or buy and spin cotton thread; then (2) other communities are responsible for staining: at the coast, with snail (*Plicopurpura pansa* Gould) or indigo dye (from plants species *Indigofera suffruticosa* Mill. and *I. tinctoria* L.) and at the central valleys, with crimsom cochineal (*Dactylopius coccus* Costa, an insect pest of cacti); afterward (3) thread is transported for waving, usually with horizontal or rigid loom and; finally (4) textiles are used by indigenous communities or conveyed to obtain a fair price for this work [25].

Remigio Mestas has contributed to the formation of the network by finding the just price and sustainable use of traditional textiles [25]. In addition, scholars and social fighters support the preservation of culture and natural resources like Dr. Alejandro de Ávila (Oaxaca Ethnobotanical Garden director and advisor and curator of the Textile Museum of Oaxaca) or artist Francisco Toledo (founder of the

Center for the Arts and Textiles of Oaxaca), and several businessmen and intellectuals promote the protection of cultural roots and a healthy environment.

The Textile Museum of Oaxaca is one of the successes of these efforts. Founded by the Alfredo Harp Helú Foundation, the Museum has the purpose of preserving regional handicrafts in a space that allows exalting the testimonies of textile history [26]. In this sense, textiles are presented not only as clothes but also as a means to display and perceive the feelings, illusions, myths, beliefs, and experiences of the communities that produce them [26].

Government initiatives also support the conservation of these traditions like the Museum of Popular Arts of Oaxaca under the National Council for Culture and the Arts (CONACULTA), or the National Commission for the Knowledge and Use of Biodiversity (CONABIO) that recently conducted a cultural map entitled "Threads from the land of clouds" a photographic exhibition that brings cultural richness of the fabrics and textiles of the Oaxacan people.

Medicinal Uses

Although cotton usage is mainly known for textiles and all the activities surrounding its production and commerce, the plant also presents applications in traditional medicine. Yucatecan Maya had many medicinal uses for the cotton plant (which they call *taman*): crushed young shoots were used for asthma; crushed seeds were taken for tenesmus and aching bones. Convulsions were treated in a bath of boiled leaves; the blossom was used to cure earache; and the toasted leaf is squeezed into the eye to stop twitching. In addition, scalp diseases were treated with hot crushed flowers; ulcers and other skin diseases were treated with crushed leaves; and "a certain veneral disease" was treated with the flowers of the cotton plant. The pulverized stem was used to relieve ulcers, and bites of scorpions, snakes, and other venomous creatures were cured "admirably" with crushed plants probably young. Other non-Mesoamerican groups used parts of the cotton plant for food. The Pima, for example, used the seeds as food, pounding them up with mesquite beans in a mortar, or parching and eating them without grinding. While such a use is undocumented for ancient Mexico, toasted cottonseeds were used for food in twentieth-century Tepoztlan [21].

In Quintana Roo and Tabasco, the disease most commonly treated with cotton is cough, by taking diluted sap from leaves in water and juice from roasted fruits, or seeds boiled in water or mixed with purple maguey or St. Nicholas herb (*Piqueria trinervia* Cav.) to make a potion. Cotton also often is used in the treatment of other respiratory diseases such as asthma, colds, throat clearing, and labored breathing that produces in the patient's chest a whistle; for these, the leaves are roasted and are applied, together with their juice, on the chest. Furthermore, this plant can be used to aid in childbirth or menstrual disorders, wounds, sores, scorpion stings, or snake bites and to lower blood pressure or fever. Traditional medicinal uses are mentioned both in the north of Mexico, especially in Sonora, and in the southern States [27].

Modern Uses of *Gossypium hirsutum*

Cotton today has a diversity of applications, principally medicinal and many more such as pigments, derivatives for cattle feed, different uses of the oily extracts, among others.

Gossypol Applications

Gossypol is a molecule that occurs in cotton and its relatives of the genus *Gossypium*. The quantity in which it occurs varies between species, varieties, and organs of plants (e.g., it is higher in the seeds than in the roots) depending on the fertilization, cultivation conditions, and the pressure exerted by insects (Fig. 18.2) [28].

The gossypol molecule can react differently according to the situation. It is said that gossypol has a complex chemical reactivity, and this is reflected in the different classes of enzymes that can be inhibited by its presence, particularly those engaged in the processes of production and transportation of energy in cells, and therefore this compound can be attributed to large variety of biological effects such as antitumor activity, spermicidal, antimalarial, antiparasitic, antiviral, antiamoebic, and other activities [29–31].

Gossypol is produced by a mixture of pairs of compounds called enantiomers, where one is called (+) and the other (−), because their images are opposite and cannot be placed identically one above the other, like the images of our hands; the shape is the same when both palms or backs come together but are not superimposable when different faces come together. These gossypol enantiomers have different biological activities. The (−) enantiomer is quite toxic to most animals, including mammals; only in ruminants toxicity is lower (e.g., herbivores such as giraffes, deer, cows, and goats), and it is even lower in male ruminants than in females. This difference of gossypol toxicity between sexes is something that was noted for some time in many mammals [32]. The presence of gossypol gives protection to the plants from predators such as insects, voles, and raccoons that otherwise might feed on these plants and their seeds [28, 33].

Cottonseed

The most common destination of cottonseed is cattle feed; however, the by-products obtained during its industrial processing have many different and profitable uses.

Fig. 18.2 Gossypol glands occur widely throughout plant structures of all *Gossypium* species. Gossypol glands are easily recognized as the black dots over the plant tissues. *Upper left*: *G. hirsutum* leaf. *Upper right*: *G. hirsutum* stems. *Center left*: *G. hirsutum* leaf (detail). *Center right*: *G. thurberi* leaf. *Lower left*: *G. turneri* flower (observe glands over pistil). *Lower right*: *G. turneri* young fruit

Cottonseed processing starts with cleaning and could stop with the extraction of gossypol for drugs and highly industrialized processes. The cleaning involves removing foreign matter such as leaves, stems, or dirt. Then, removal of the smallest and finest fiber that remains attached to the seeds after the gin (where long fibers are separated to make textiles) takes place. It is normal that this step happens twice because each time has different targets: longer fibers are removed the first time and the second; fine fibers are recovered mainly to produce quality paper for currency and art. Natural fibers such as linen and cotton can bind strongly than cellulose which is why the paper made with both fibers can bear the mistreatments plain paper cannot. Each dollar bill is made of 75 % cotton and 25 % linen, and in 2011 to produce a dollar cost 9.6 cents [34].

After the husk is removed, cottonseed is preferred by the dairy industry as cattle feed although it has been tested in pigs [35], chickens [36], and rabbits [37] among others, and the best response decreases the weight, so it's always negative. Seeds are ground and then mixed with cottonseed flour to give more body and ease of handling, but they also have many other industrial uses such as plastic manufacture, oil drilling (mud additive), and furfural production (a solvent used in plastic and synthetic rubber production and in petroleum refining).

When embryos are left bare, called the bait of the seed, their main use is to make flakes with chemical and mechanical processes to slightly decrease the amount of free gossypol [38]. Oil extraction is mainly done with organic solvents (usually hexane) and recovered to produce crude cottonseed oil, which then goes through a refining process to separate completely the oil from the free fatty acids. The cottonseed oil extracted is subsequently refined to produce products such as cooking oil, margarine, and shortening. This oil was the most popular in the United States and in the world before World War II, then was replaced by soybean and canola [39].

When the process of extracting oils is over, lipid content in flakes has decreased to less than 0.6 %. The flakes are then toasted to evaporate compounds (added) and ground into flour. Often, some of the compounds refined are returned to the flour to enhance its energy content or sometimes vitamins and minerals are added, depending on the final destination. After leaving the toaster, flakes are known as cottonseed flour. This flour is dried, cooled, and ground or can be processed into pellets [40].

In Mexico, ranches engaged in milk production are the major customers of this seed. These ranches store seeds preferably in ventilated and cool conditions to prevent fires because in case of fire the highly flammable fat content from the seeds can cause large amounts of seed to be lost. However, these storage and transport conditions favor the spread and escape of cotton plants. There is a legal misunderstanding in Mexico where genetically modified seeds are treated and sold as conventional [20, 41], forgetting that they are still living organisms that can germinate and reproduce when conditions are appropriate; 3 % of the seeds a cow can eat are still viable when they come out of the digestive tract and therefore continue their development to become an adult plant. The people who manage these seeds are unaware that they have a seed in their hands that can cause at least one of the four most common types of damage caused by GMOs: (1) The damage associated with the movement of genes and subsequent expression in different organisms and species; (2) damage directly or indirectly associated with genetically modified organisms; (3) damage to nontarget organisms, which are those for which the transgene was not designed or that are not the subject for which the GMO was released; and (4) can even affect the evolution of pest resistance, hindering the strategies for pest control [42]. In short, it is very important to achieve a way to change the perspective on the cost to reverse these impacts. Destroying the seed by taking into action production processes of greater economic impact, turning them into an advantage that will also develop a biosecurity tool and will even exploit both natural and financial resources invested in the crop.

Medicinal Uses

Apparently, the people in China have long known the abortive properties of the plant and its effects on men sperm; however, it was later noted that families who cooked with cottonseed oil had fewer children, which triggered scientific studies of the case. Studies intensified in 1970 in China, Brazil, and Nigeria, but only the last two continued to improve protocols, despite contraceptive effectiveness was clearly irreparable and side effects like infertility and lack of absorption of potassium were serious. However, some researchers still think that the effects can be improved with dietary changes and smaller doses for men who no longer wish to reproduce [43]. Furthermore, these studies were very important because they helped to learn more about a molecule (i.e., gossypol) that could have many potential uses, as diminish or affect the growth of cells is what is sought in cancer and antiparasitic treatments.

Since 1989, potential treatments were tested in vitro to control the human immunodeficiency virus (HIV) to reduce their enzymatic activities [44] with (−) gossypol [45]. It can be used ingested, as well as vaginal gels for HIV control, in addition to their effect to stop the mobility of sperms that serves as birth control and even to prevent other sexually transmitted diseases such as herpes [44, 46]. Gossypol is one of the most effective ingredients, both in traditional pharmaceutical preparations and alternative medicine.

Conclusions

After a review of past, current, and potential uses of cotton in Mesoamerica is clear that conservation strategies of both, plants and practices, is possible with dedication, availability of information and public policies oriented to the comprehensive conservation of plant genetic resources in situ. The regard for the laws that rule the respect for the rights, dignity, natural resources, and territories of indigenous peoples, taking into account their culture and traditions, are fundamental to achieve this goal, but also a well-informed society is essential to allow fair payment for their work and their products. Increase the estimation of the young generations for the work of the elderly will permit the continuity of sustainable development efforts. Similar organized efforts are probably emerging in Oaxaca, as we presented as an example. These endeavors are fundamental because they arise from society and may endure for long-term although they may require the support of governmental and non-governmental organizations.

The most sophisticated uses of cotton are generally associated with intensive monoculture, a practice that is possible in Mesoamerica only in a small percentage; however, the information can be used at different scales. Domesticated and genetically modified plants can sustain gene flow with wild relatives and traditional and organic and crops, causing damage to diversity. Nevertheless, exploitation of the entire seed will generate a measure of biosecurity to prevent dispersion and in turn produce significant profit. Descriptions about this process are abundant in this chapter and in the literature, so they could make them attractive to the industry and facilitate their implementation.

In general, it is clear that the variety of traditional medicinal uses of cotton is due to the active compounds that have been described and used in recent decades by modern medicine. Surely, when the control of the toxic effects of gossypol is achieved, applications on human health issues will increase, but for now we present the available information to promote the surge of new ideas.

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Chapter 19
An Interdisciplinary Perspective on the Loss of Traditional Ecological Knowledge (TEK) in the Tehuantepec Isthmus, Oaxaca

Alfredo Saynes-Vásquez, Francisco Vergara-Silva, and Javier Caballero

Abstract Research on traditional ecological knowledge (TEK) in Mexico is linked to geographical regions with the highest levels of biocultural diversity—for instance, Chiapas, Oaxaca, and Yucatán. Long-term historical and ethnographic research in Oaxaca suggests extensive interethnic conflict during precolonial times and subsequent Western interventions in colonial and postcolonial contexts, which might have contributed to knowledge loss in specific linguistic domains that have been the focus of classical ethnobiological studies—e.g., plant names. Here, we review some of the principal findings of a quantitative ethnobotany project carried out during the past decade on the loss of botanical knowledge in Zapotec communities located in the Tehuantepec Isthmus, and connect its conclusions to previous ethnobotanical and sociolinguistic research in the area. We discuss the scope of future investigations oriented to establish a link between historically informed cognitive anthropology/ethnobiology, comparative linguistics and TEK research in Oaxaca, and comment on some ethico-political dimensions of ethnobiology in the Tehuantepec Isthmus.

Keywords TEK • Tehuantepec Isthmus • Zapotecs • Cultural displacement

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Introduction

Historical, Economical, and Ecological Context

The Isthmus of Tehuantepec has been a region of multiple prehispanic contacts involving different ethnic groups, including Maya, Huave, Chontal, Zoque, Mixe, and Zapotec [1]. At times, these contacts ended in wars for the appropriation of natural resources, given the strategic location of the area for trade routes. Even after the occupation of the Isthmus by the aforementioned groups, Aztec and Mixtec groups fought each other to control the area until the arrival of the Spaniards [1]. Thus, the Isthmus acquired geopolitical importance since precolonial times, and although colonial centralism somewhat eclipsed this status, the importance of the region has been revived in the early nineteenth century, a situation which has not declined until today [2].

After Mexico's independence, the Tehuantepec Isthmus has been subject to successive cycles of development with the aim of integrating the region to the *vida nacional* (i.e., the Mexican State plans for the achievement of material progress in underdeveloped, "backwards" areas of the country). The construction of a large railroads system, by the end of the nineteenth century, was one of those great development projects; after its inauguration in 1894, it immediately favored a series of development inequalities involving different populations. Juchitán is not placed along the main railroad line; therefore, the towns that resulted most affected by these progressively unequal commercial exchanges were Ixtepec, Tehuantepec, and Salina Cruz [2]. Up to 1910, both Juchitán and—to a lesser extent—Tehuantepec were considered as "the state's barns" but, due to climate and society dinamics-related phenomena—e.g., droughts and the mobilization of labor—such status was lost. After the food production crisis, corn commercialization was even prohibited outside of the Juchitán district and *trueque* (barter) returned as a form of alimentary products exchange [3].

Between 1950 and 1960, 70–75 % of the economically active populations in the Isthmus were engaged in subsistence agriculture [4]. In contrast, according to the national census of 2000, the population involved in primary activities ranged only from 1.5 to 13 % [5]. Apparently and paradoxically, this phenomenon is the result of the construction of the Benito Juárez dam, which opened in 1962. After the construction of this dam, a process of speculation and monopolization of land was triggered; also, the Mexican State encouraged cash crops of rice, sugarcane, as well as improved varieties of maize and, more recently, sorghum. This phenomenon of technological modernization, coupled with the incentives and facilities offered by the government, increased the pressure for the clearing of the forest, with the consequent reduction of the original vegetation coverage [6, 7]. In turn, this chain of events let tosocial unrest and political discontent inside and between the municipalities that share the dam [8, 9]. Today, much of the land cleared during the period 1960–1980 is only used as pasture for cattle.

According to the *Atlas Regional del Istmo de Tehuantepec* [10], change of land use caused a reduction of the original vegetation of the region, down to a value of 49.74 % (in 1970). By 2000, this area had decreased to 35.17 % [10]. This suggests that the policy of national integration has been a major cause of the loss of the natural environment, as well as a factor behind the displacement of economic activities (from primary towards secondary and tertiary). This historical process places the Tehuantepec Isthmus as a privileged site where the effect of the globalization process on the cultures and languages of indigenous communities can be studied.

Defining Traditional Ecological Knowledge, Cultural Change, and Cultural Displacement

We focus our analyses on the complex effects that negatively impact on what throughout this chapter will be formally called *traditional ecological knowledge* (TEK) [11–17]. TEK refers to the knowledge, practices, and beliefs link to relationships between human societies and their physical, biotic, and cultural environments [18]. This knowledge is the result of a long history of interactions between societies and nature, it is unique to each culture, and involves the conceptual and practical recognition of natural resources, food chains, successional dynamics, and soil and water management, among others. The development of TEK changes with the availability of environmental resources, as well as the needs of local communities in the contexts of their contacts with culturally divergent groups [19, 20].

Defining Cultural Change

Cultural change and the related concept of *cultural displacement* are also important interpretive tools in this work. We define these notions as the processes of acquisition of tastes and urban values, associated to the loss of local languages and the abandonment of local agricultural practices and primary production (or the modernization of the latter), which in turn correlate with loss of TEK. The idea of cultural displacement developed here derives from a previous quantitative ethnobotanical study, undertaken in three Zapotec localities in the vicinities of the Tehuantepec Isthmus—namely, San Blas Atempa, Santa María Xadani, and Juchitán de Zaragoza ([21]; Fig. 19.1). That study is part of a long-term ethnobiological research project—in the tradition of “cognitive studies in ethnobiology” (*sensu* [22])—the first stage of which was recently the basis of a Ph.D. thesis defended at the National Autonomous University of Mexico [23]. The evidences collected and analyzed in the aforementioned research indicate that (a) the level of linguistic competence in the local language, as well as (b) economic activity and (c) the degree of schooling are the most significant causes behind the loss of TEK. These findings agree with those of many other international ethnobiological studies [14, 15, 24–31].

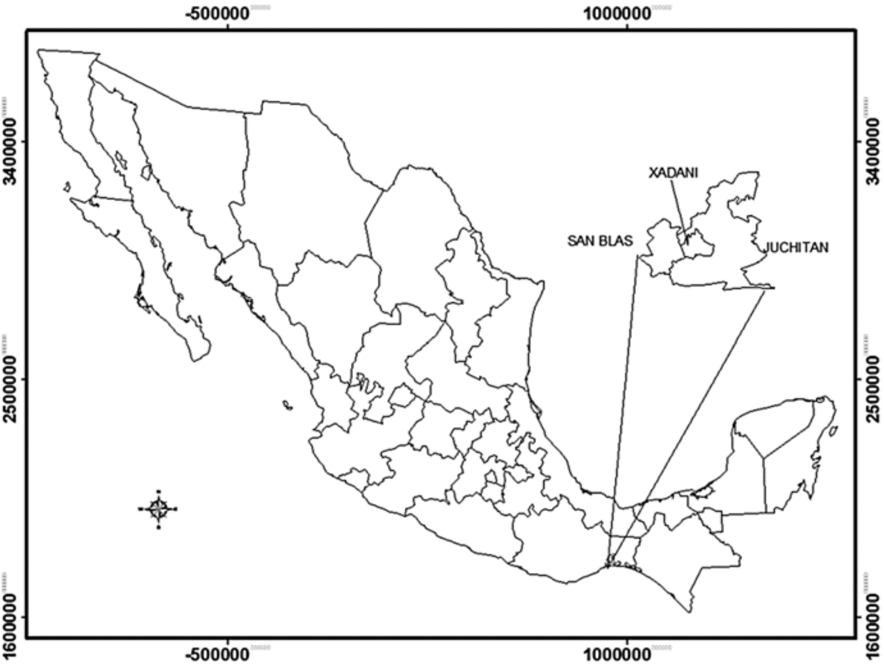

Fig. 19.1 Location of the study sites

What Causes the Loss of TEK?

Given that knowledge in traditional societies is based on its relationship with the environment, it is elemental to think that the destruction of the ecosystems in which these societies live might lead to the loss of that knowledge. Absence of the "object" of traditional, local knowledge could thus cause societal transformation or, in extreme cases, lead to its collapse—as in the case of the Anazasi (southeastern United States) or the Easter Islanders [32]. In the Juchitán municipality, the formerly mixed Zapotec-Spanish names that used to be assigned to *secciones* (i.e., divisions or neighborhoods) started a process of erosion some 40 years ago, and are currently named just by Spanish words. This linguistic phenomenon can be closely correlated with the disappearance of specific plant taxa—for example, the section formerly called *Primera-beu* ("First-beu") coincided with the natural distribution area of the **beu'** (*Vitex mollis* Kunth), a plant whose fruits were used to prepare a sweet [33]. Currently, there are no **beu'** trees left, and therefore the name of the plant and the sweet are missing.

On the other hand, culture plays an important role in the way in which traditional societies relate to their environment. An interesting case in the villages of the Tehuantepec Isthmus has been the phenomenon triggered by the introduction of beer in the early sixties of the twentieth century. Along with alcoholic drinks for the party, beer companies offered free chairs or tables, installing roofs (made of metal or plastic) with columns. This innovation represented a shift from the construction of *enramadas* (shelter-like structures) made from local bamboo or palm species. The complex process of shelter construction—which involved supervision by elders—was also dismantled, and the associated weaving technique lost [34].

The integration of local lifestyles to the standards imposed by national, state-owned institutions, the imposition of the Spanish language as *lingua franca*, and the increase in levels of schooling have all been important elements that negatively influence the maintenance of TEK. As argued in the Introduction, historiographic approaches to the Tehuantepec Isthmus indicate that changes in TEK can be traced back to colonial and precolonial times; a conspicuous example is that of numerals. As in other Mesoamerican cultures previous to the colonial period, the Zapotec count system was vigesimal; today, counting is decimal. Some numbers have been lost or remain as archaisms—for instance, number 15 was **chiiñu'** in ancient Zapotec [35].

How is knowledge lost in the botanical and other biology-related cognitive domains in the Tehuantepec Isthmus? The answer is not simple. Some Zapotec plant names are not completely lost, but they are partially composed of Spanish words—e.g., the green tomato, whose Zapotec name was **bichooxhe ndaaba'** (tomato with clothes), is now called **green bichooxhe**; a rib (*costilla*, in Spanish), being part of the human body, was named **dxita binni** in Zapotec, but is now called **dxita binni costia**. Items and associated practices which are being lost in the communities studied here are weaving palm (*Sabal mexicana* Mart.), artisanal sandals (*huaraches*), hand-made tortillas, the construction of water wells, and houses built with local techniques. In addition, adobe has been replaced by cement blocks, and roof tiles and palms also by cement. These examples are evidence of the phenomenon that Berlin [36] referred to as *involution*, which assumes the loss of vocabulary in specific areas of social life because certain activities reduce their societal importance. It is worth mentioning that, in the face of such socioeconomic and cultural changes, collective memory is maintained in the Tehuantepec Isthmus. This memory remains in spite of more recently established innovations, though limited to small redoubts if not to just a few individuals.

Results

Zapotec Botanical Classification: Main Features

As a conclusion of the initial stages [21, 23] of the research project described here, a model of the local botanical classification was proposed. In this model, there is no individual word to designate a unique beginner "plant"; instead, four different classes (i.e., groups) were found to define the life-form—namely, **yaga** for tree, **luba'** for vines, **guixi** for herbs, and **guie'** for flower. The latter category, **guie'**, is a taxon recognized by the communities studied; these communities also recognized generic, specific, and varietal taxa (Table 19.1). In the plant classification of the Isthmus Zapotec, the unique beginner (i.e., the sole initiator) is not named—i.e., there is no term to name the Zapotec "plant" concept. This feature is shared with

Table 19.1 Taxonomic hierarchies in Tehuantepec Isthmus Zapotec plants

Life-form	Generic	Specific	Variety
Yaga (tree)	**Yaga biquiiche** (*Pithecellobium* sp.)	**Yaga biquiiche beedxe'** (árbol de biquiiche beedxe'; *Pithecellobium lanceolatum* (Willd.) Benth.)	
Luba' (vine)	**Luba' bacuxu** (*Antigonon* sp.)	**Luba' bacuxu blancu** (*Antigonon flavescens* S. Watson)	
Guixi (herb)	**Xuba'** (*Zea mays* L.)	**Xuba' huiini'** (Maíz chico; *Zea mays* L.)	Xuba' huiini' moradu
Guie' (flower)	**Guie' chachi** (cacalosúchitl; *Plumeria rubra* L.)	**Guie' chaachi gui'xhi'** "wild cacalosúchitl" *Plumeria rubra L.*	

other languages and does not necessarily mean that plants are not recognized as a conceptual category [22].

Names given to plants and animals in local models of classification have a close relationship with the reality that people see in their environment and show how living beings are conceptualized [37]. Most of the Spanish language influence in Zapotec plant names is noticeable for introduced species, through the substitution of a particle in a Zapotec word for a Spanish one. An example is *estropajo*, which is named **Luba' estropaju** (*Luffa aegyptiaca* Mill.) in Zapotec. On the other hand, we find some local species whose specific epithets are named in Spanish, especially in relation to color—e.g., **Luba' bacuxu blancu** (*Antigonon flavescens* S. Watson; *blanco* is Spanish for "white"), **Luba' bacuxu moradu** (*Antigonon cinarescens* M. Martens & Galeotti), and **Lasa yuu moradu** (*Melochia pyramidata* L.). In the latter two cases, *morado* is Spanish for "purple"; in all three instances, the word for colors is "zapotecized" (i.e., the "o" is substituted by "u"). Other examples are **Yaga cruu** (*Randia* spp.; *cruz* is Spanish for "cross") and **Luba' sombreru** (for a species of Convolvulaceae; *sombrero* is Spanish for "hat"). All the previous examples illustrate the so-called syncretic project of Hill and Hill [38]—that is, the strategy of speakers of a minority language in conflict, who resort to loans (borrowings) of various linguistic materials (in this case from Spanish) to maintain structure of the local classification, but not the original nomenclature.

Ideology

It is important to point out that, at the localities studied, people want to know the Spanish names of plants regardless of their existence in Zapotec. An explanation for this attitude is related to the higher social status acquired by Spanish speakers, or by those who know Spanish names for plants; this phenomenon was recognized by Hill and Hill [38] in central Mexico and by Saynes-Vázquez [33] in Juchitán. These data point to a dual problem in relation to language reproduction: on the one hand, to speak Spanish provides status; on the other, certain inability to speak Zapotec induces speakers to reinforce verbal inhibitions. We interpret these features as indications of the presence of ideologies associated to presumed "linguistic purity"; according to Hill and Hill [38] and Moctezuma [39], such purism concerning language acts in detriment of the reproduction of the latter. In addition, some studies have found that, in traditional communities, women's linguistic behaviors change more by learning a second language and transmitting it to their children [40, 41].

Some introduced plant species are named with the Zapotec names of a phylogenetically related species, or the names are assigned according to physiognomic resemblance. This phenomenon of displacement or "usurpation" of the local name has been reported by Berlin among the Tzeltals of Chiapas (according to Hunn [42]). The latter author states that the same phenomenon occurs among the Zapotecs of San Juan Mixtepec (Oaxaca).

Quantitative Assessments of TEK Loss

Saynes-Vásquez [23] proposed and evaluated an index of cultural change, based on data collected from a group of 300 male respondents from three Zapotec-speaking communities located in the Tehuantepec Isthmus (see Introduction). All respondents provided information through the application of a questionnaire involving a series of sociodemographic data items, such as age, schooling, economic activity, linguistic competence in Zapotec and Spanish, as well as address. Standard principal component analysis (PCA) was the statistical tool of preference to analyze this data set (for additional methodological details, see Saynes-Vásquez [21, 23]). The score associated to each respondent along the first principal component was interpreted directly as the index of cultural change (Fig. 19.2). The PCA results

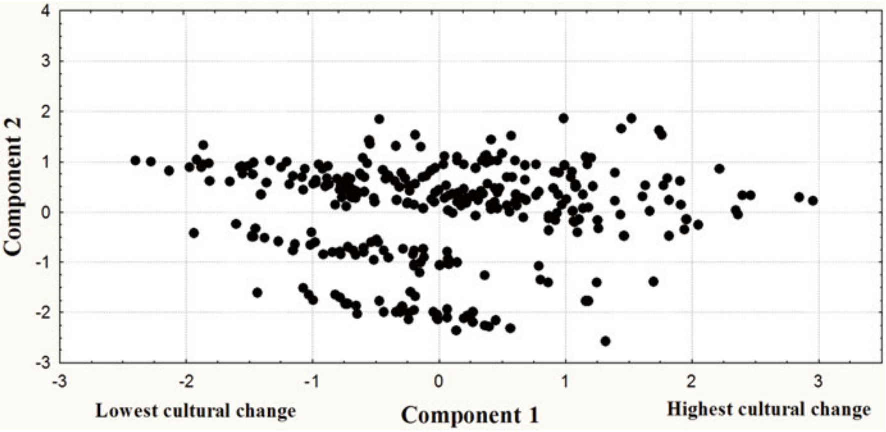

Fig. 19.2 Ordination of the 300 heads of family interviewed, according to seven social and demographic variables. Subsistence workers with a low degree of formal education and less fluency in Spanish are located on the extreme left side of the classification axis (*negative values*); in turn, respondents involved in secondary and tertiary activities were located on the opposite extreme (*positive values*). Taken from [21]

Table 19.2 Results of the principal component analysis (PCA) of the 300 heads of family

Variable	Component 1
Municipality	0.106
Occupation	**0.780**
Age	–0.343
Schooling	**0.812**
Understands Spanish	**0.712**
Speaks Spanish	**0.831**
Speaks Zapotec	–0.108

The values of the most important social and demographic variables are indicated in bold characters. *Extraction method*: principal component analysis. *Rotation method*: Varimax normalization with Kaiser. Rotation converged in three iterations. Taken from [21]

additionally suggest that ability to speak and understand Spanish, degree of schooling, productive activity, and/or occupation are the most important variables that define the first component (Table 19.2).

The cultural change index was then correlated with the results of a test of competence in Zapotec botanical nomenclature, focused on knowledge at different taxonomic levels—namely, visual recognition, knowledge of growth form, knowledge of generic and specific names, and knowledge of uses. The sum of this second set of quantifications was integrated as a global index. A negative correlation between the index of cultural displacement and all levels of knowledge tested was obtained.

Descriptive Data Statistics of Competence in Botanical Nomenclature Knowledge

Raw data showing a decreasing competence in botanical knowledge as a function of increasing difficulties in Zapotec plant naming practices are shown in Table 19.3. Competence in this knowledge is higher at visual recognition, as it does not involve a sophisticated awareness of the environment, neither a high competence in the local language. Among Tehuantepec Isthmus Zapotecs, a strong, negative correlation between the index of cultural displacement and the scores at all levels evaluated was observed for the 300 respondents, with R^2 values between 83.1 and 88.3 % ([21], Fig. 19.3). Table 19.4 shows that respondents who belong to the primary activity group recognize more plant names than the other group at all levels tested. Table 19.5 further shows that this difference is statistically significant; both analyses indicate that economic activity is strongly associated with loss of TEK. Overall, these data are consistent with results found by other authors [11, 26, 29], and they can be associated with processes of economic development and with displacements of the local language and culture.

Table 19.3 Statistics of the levels of knowledge

Variable	Mean	Standard deviation	Coefficient of variation (%)
Competence in visual recognition	23.72	6.057	25.53
Competence in recognition of growth form	23.39	6.389	27.31
Competence in recognition of generic name	20.59	7.673	37.26
Competence in recognition of specific name	18.52	8.594	46.40
Competence in knowledge of use	18.22	7.148	39.23
Global index	104.45	35.06	33.57

Mean, standard deviations and coefficients of variation are shown for each degree of knowledge on a regional scale

Conclusions

A Historically Informed, Quantitative Ethnobotanical Assessment of the Loss of TEK in the Tehuantepec Isthmus, Oaxaca

Throughout their precolonial, colonial, and postcolonial historical trajectories, non-Western, traditional societies have generated classifications in various domains of knowledge, including the one properly concerned with animals, plants, and other living beings [22]. Beyond its identification by certain major strands of anthropological theory—for instance, structuralist and post-structuralist approaches (e.g., [43, 44])—such biological knowledge domain is crucial to articulate the technical concept of *traditional ecological knowledge* (TEK), an ethnobiology and cognitive anthropology notion that proves indispensable to interpret the results of ethnobotanical studies conducted in regions with high degrees of biocultural diversity [11–18]. Besides its theoretical importance in ethnobotany, we argue that TEK is also useful in interdisciplinary studies aimed to understand the influence (especially during the twentieth century) of the political and economic contexts that have shaped social life in Mesoamerican regions like the Tehuantepec Isthmus. This area was chosen for the ethnobotanical research project conducted by the first author of this chapter, the main results of which [21, 23] have been briefly summarized here.

Socioeconomic and cultural transformations in the Tehuantepec Isthmus have left a profound mark in the ecology of the region [2, 7]. Early in the twentieth century, the construction of the trans-Isthmus railroad—which was intended to increase and improve international trade as well as movement of goods and local people—stimulated the formation of several urban centers, like Ixtepec and Salina Cruz. Regional development initiatives began to decline after the start of the Panama Channel operations in 1914, but new interventions and consequences were to come later. During the construction of the Pan American Highway, between 1942 and 1947, a burst of population growth took place along with the emergence of a market for building construction and associated services, slowly changing the previously

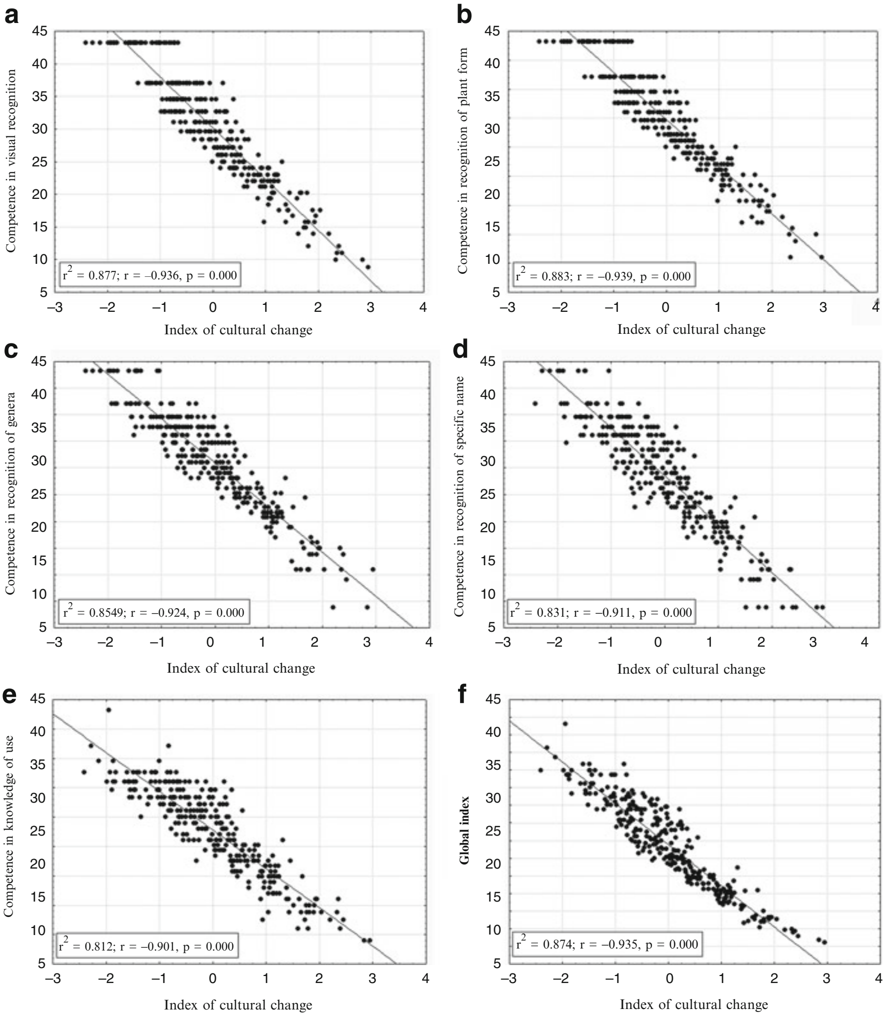

Fig. 19.3 Regressions on the index of cultural change at all levels of knowledge competence. (**a**) Competence in visual recognition, (**b**) competence in recognition of growth form, (**c**) competence in recognition of generic name, (**d**) competence in recognition of specific name, (**e**) competence in knowledge of uses and (**f**) global index (integrating all values). Taken from [21]

dominant rural system of simple social reproduction. From the 1950s onwards, occupancy levels in primary economic activities decreased significantly, in ways that justify speaking of structural and economic change [4, 9, 45].

On the other hand, although hydraulic works were initiated in the 1940s—to take a more public form in 1946 with the inauguration of the first dam, called Las Pilas—it was not until the opening (in 1961) of the Benito Juárez dam, in the Jalapa del Marqués area, that the massive process of deforestation of more than 53,000

Table 19.4 Statistics of knowledge levels at regional scale

		Competence in visual recognition	Competence in recognition of growth form	Competence in recognition of genera	Competence in recognition of specific name	Competence in knowledge of use	Global index
Primary activity	N	150	150	150	150	150	150
	Mean	*28.22*	*28.13*	*26.48*	*25.29*	*23.80*	*131.920*
	Std. Dev.	1.706	1.773	2.548	3.428	2.761	10.9111
Secondary and tertiary activity	N	150	150	150	150	150	150
	Mean	*19.23*	*18.65*	*14.71*	*11.75*	*12.65*	*76.9867*
	Std. Dev.	5.476	5.796	6.471	6.646	5.682	28.8066
Total	N	300	300	300	300	300	300
	Mean	*23.72*	*23.39*	*20.59*	*18.52*	*18.22*	*104.453*
	Std. Dev.	6.057	6.389	7.673	8.594	7.148	35.0684
	Coefficient of variation (%)	*25.53*	*27.31*	*37.26*	*46.40*	*39.23*	*33.57*

Table 19.5 Results of the *t*-test for independent samples, showing the statistical significance of differences between groups of economic activities, as defined in Table 19.4

Independent samples test

		Levene's test for equality of variances		*t*-test for equality of means						
		F	Sig.	t	df	Sig. (2-tailed)	Mean difference	Std. error difference	95 % confidence interval of the difference	
									Upper	Lower
Competence in visual recognition	Equal variances assumed	0.758	0.385	21.36	298	*0.000*	12.977	0.6073	11.782	14.173
	Equal variances not assumed			21.36	290.72	*0.000*	12.977	0.6073	11.782	14.173
Competence in recognition of growth form	Equal variances assumed	1.163	.282	21.38	298	*0.000*	13.395	0.6264	12.162	14.628
	Equal variances not assumed			21.38	288.64	*0.000*	13.395	0.6264	12.162	14.628
Competence in recognition of generic name	Equal variances assumed	12.81	0.000	20.76	298	*0.000*	13.874	0.6681	12.559	15.188
	Equal variances not assumed			20.76	274.18	*0.000*	13.874	0.6681	12.558	15.189
Competence in recognition of specific name	Equal variances assumed	12.55	0.000	20.79	298	*0.000*	15.225	0.7322	13.784	16.661
	Equal variances not assumed			20.79	273.22	*0.000*	15.225	0.7322	13.783	16.666
Competence in knowledge of use	Equal variances assumed	28.67	0.000	21.40	298	*0.000*	11.376	0.5315	10.330	12.422
	Equal variances not assumed			21.40	253.54	*0.000*	11.376	0.5315	10.329	12.423
Global index	Equal variances assumed	0.933	0.335	23.79	298	*0.000*	8.0871	0.3399	7.4181	8.756
	Equal variances not assumed			23.79	295.20	*0.000*	8.087	0.3399	7.4181	8.756

hectares of dry forests took place [7, 46]. Besides this impact on the local vegetation, this event also marked the start of an economic speculation cycle upon land value [8]. Despite the existence of a 1964 presidential resolution that recognized the assignment of 68,000 hectares of communal territories to the Santa María Xadani, San Blas Atempa, El Espinal, Juchitán, and Unión Hidalgo municipalities [9] speculation, and concomitant land privatization continued. This process further contributed to disarticulate institutions as well as collective forms of participation and decision-making, up to the present [46], therefore affecting local knowledge transmission intrinsically linked to the use of Zapotec. This problem deepened in connection to an absence, after 1974, of elections of *comisariados de bienes comunales* (officers of communal lands), which has favored ambiguities in land administration [4]. The aforementioned modernization tendencies have had an effect on social reproduction mechanisms, in the sense of Parrish [47] and Campbell [9]. According to these authors, these processes led to further changes in (i) the continuity and replication of the workforce, (ii) the division of labor and class relations, (iii) biological and demographic reproduction as well as (iv) the transmission of cultural beliefs and practices and, ultimately, (v) ethnic identity and gender relations. Ongoing eolic energy-related *megaproyectos* (projects involving exorbitant money investments) are further contributing to these changes.

Last but not least, schooling is another sphere that has endured severe transformations in the Tehuantepec Isthmus, especially during the presidential period of Lázaro Cárdenas (1934–1940). In a revealing anecdote, this politician stated (in one of his traveller's notebooks) that in occasion of his arrival to power, he would send a special educational mission to the Isthmus towns, in order to establish industrial schools in Juchitán [3]. As shown by other authors [14, 28, 30], schooling is one of the salient variables in the process of traditional knowledge loss, especially when it comes to botanical nomenclature. This has been elsewhere demonstrated by Zent [27, 48] among the Piaroa of Venezuela, and by Cortés-González [49] after his work with the Nizanda Zapotecs. According to the estimation of the cultural displacement index (see Results), schooling had a weight of 0.812 in the first component of the PCA analyses, just below linguistic competence in Spanish (with a weight of 0.831 in the PCAs). Performing a simple correlation between the global knowledge index and the schooling grade of all respondents, the determination coefficient was 0.42; in a similar exercise exclusively involving ages, this coefficient had a value of 0.14. This numerical difference points to a secondary importance of the age factor; however, it should be reminded that age as a variable has also been linked to the knowledge acquisition process under ethnobiological research conditions in separate studies performed in Mexico (e.g., [50]). According to Zent [27, 48] and Cortés-González [49], individual knowledge of local plant names has been mostly acquired when individuals have reached 30 years of age. Given that on average, the age of respondents in the present study was 48.6 years, we conclude that schooling is placed high among the sociodemographic variables evaluated in the research project summarized here (see Table 19.2) in a hierarchy of putative causal factors associated with the loss of TEK in the Zapotec communities under study.

Prospects: Biological Cognition, Sociohistorical Linguistics, and Ethico-Political Reflexivity

An evidently underexplored aspect of the work summarized here has to do with *biological cognition*—i.e., the central idea around which ethnoscientists Scott Atran and Douglas Medin have developed the latest stage of their earlier field research on "folkbiology" [19]. To paraphrase their formulation in *The Native Mind and the Cultural Construction of Nature* [51], a continuation of the work presented here should involve asking which are "the cognitive consequences of reduced contact with nature" in Zapotec communities. Atran and Medin [51] have proposed the concept of *devolution,* defined as "a decrease in knowledge about living kinds." Is devolution useful to better understand loss of TEK, as elaborated in our historically informed, quantitative ethnobotanical perspective? And, what do studies like Saynes-Vásquez et al. ([21]; see also [23]); contribute to understand the universal features or properties of biological cognition?

As noted earlier, *cultural displacement*—an analytical category here developed out of the notion of cultural change used in Saynes-Vásquez et al. [21]—roughly converges with the concept of *linguistic displacement*, recently used by Pardo and Acevedo [52] in a thorough sociolinguistic study of the entire state of Oaxaca. These authors have enlisted a set of explanatory factors of what they define as "the result of an asymmetric contact between indigenous languages and Spanish (…) characterized from the sociology of language standpoint as diglossia." Inasmuch as they assume a historical/historiographic horizon complementary to the one depicted here—for instance, emphasizing the role of territorial reductions or displacement, as well as the importance of a decrease in the number of speakers and the asymmetries in the prestige and social function of the languages in contact—we believe that future studies that follow up on quantitative ethnobotanical approaches should look more closely at the long-term, whole-state Oaxacan sociolinguistic studies that have been published lately.

Sociolinguistic perspectives aspiring to frame models that explain the loss of competences (both synchronically and diachronically) in the many Oaxacan indigenous languages—including Zapotec variants, but certainly not limited to them—could involve Juan José Rendón's pioneering historical linguistics work (compiled in [53]). The attachment of this author to the glottochronological and lexicostatistical tradition of Morris Swadesh [54] might suggest that his idiosyncratic mix of social and historical linguistics has not much to offer to contemporary ethnobiological work in Oaxaca (for a critique of Swadesh's historical linguistics perspective, see [55]). However, we suggest that Rendón's political views (e.g., [56]) which have clear linkages with discourses on decoloniality and decolonization elaborated during the last 30 years by Oaxacan intellectuals [46, 57], deserve to be revisited in the context of debates on the ethico-political compromise that researchers would choose to establish with the communities they study. As attested by ethnography of science studies on ethnobiological research projects in Mexico [58], an important degree of reflexivity should now be expected from any specialist interested in collecting ethnobiological information of any sort in the many biologically and culturally diverse regions of Mexico. Among these areas, Oaxaca necessarily occupies a special place, anchored in studies of its precolonial, colonial, and postcolonial biocultural history.

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Chapter 20
Ethnobotany and Ex situ Conservation of Plant Genetic Resources in México

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Abstract In this chapter, the importance of ex situ conservation is discussed to safeguard plant genetic resources on relationship to its ethnobotanical relevance. It also highlights the importance of preserving the germplasm of species that are closely associated to human being. The diverse forms and intensities of human–plant relationship lead to the accumulation of traditional knowledge and the modification of the characteristics of plant populations as a result of human manipulation. When the germplasm of plant populations that are important to human being is protected, the information associated to this relationship is also protected, so that the conservation of biological diversity of useful plant species favors the protection of cultural diversity associated to its plant use. The urgency to conserve and protect the Mexican germplasm is associated to the fast and dramatic change of habitats that the country is facing.

In megadiverse countries with serious institutions, such as the Seed Bank FESI-UNAM, has undertaken efforts to conserve seeds from species of wild plants and particularly useful wild species, so that it is possible to have the raw material to carry out taxonomical, ethnobotanical, genetics, ecological and phytochemical studies and sustainable projects.

Biodiversity in Mexico

Out of the nearly 30 million species that the least conservative estimates suggest that we currently know between 10 % [1] and 12 % of the natural capital [2]. In other words, we barely know between 180,000 and 216,000 species. In Mexico, over 100,200 species have been described from the 200,000 species that are estimated [3].

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Mexico is a spectacular country. It has a highly heterogeneous territory in terms of environment and culture, which makes it one of the 17 so called "megadiverse" countries, which altogether bear around 65–70 % of the world's natural capital [3]. In its nearly two million square kilometers, the country bears diverse ecosystems ranging from humid and deciduous tropical forests to desert scrub-like vegetation to pine forests in the highlands.

According to the information provided by the IUCN [4], in the world there are 13,025 fern species, 980 gymnosperms species, 199,350 dicotyledonous species and 59,300 monocotyledonous species. Particularly, in Mexico the plant biodiversity recorded includes 21,841 Magnoliophyta species, occupying the third place worldwide, only surpassed by Brazil and Colombia [5]. The ten states of the country with the highest diversity on vascular plants are Veracruz, Chiapas, Oaxaca, Jalisco, Guerrero, Puebla, México, Michoacán, Hidalgo, and Morelos [2, 5].

In addition, Mexico shows a high endemism rate of its vascular flora, reaching up to 50.4 % with almost 11,001 species endemic to the country [5]. The richest biomes in terms of endemism are the temperate forest followed by the tropical rainforest. In particular, the highest floristic richness in Mexico is found in the temperate forest followed by the desert scrub-like vegetation and the tropical rainforest.

Unfortunately Mexico is facing a systematic deforestation and change in the land use, mainly caused by extensive cattle rising and the cultivation of a few crop species. Other factors, such as the construction of industrial complexes and highways, illegal extraction and traffic of exotic species, among other things, have also contributed to the current alarming vulnerability of many plant species of major commercial importance [6], also the vegetation has suffered extensive anthropic alterations. Very few areas of the national territory still hold unaltered ecologic communities.

Such vulnerability becomes even more critical considering the climate change, by which species are facing a number of environmental changes and their success will depend on their capacity to maintain their populations, to inhabit new zones and to generate strategies that allow them to resist different temperatures and precipitation rates [7].

Under these conditions, the alternative that brings elements to face such grave consequences over the rural productivity and the conservation of biodiversity, emerges as an urgent priority and includes the development of procedures to revert this terrible deterioration in an intelligent way [8].

Accordingly it is urgent to conserve and protect the plant germplasm of Mexico because potentially most of the species can be used for different purposes that can be identified by means of the ethnobotanical studies.

Ethnobotany

Since the origin of humanity, people used the natural resources for surviving and obtaining all the needed supplies, such as fuel, food, medicines, wood, forage, coal, oil, construction and ritual materials, among others. Consequently, since the beginning of humanity a very close bond between plants and human being was established.

Since the beginning, human being needed to know the properties and uses of plants, and on the basis of these knowledge diverse ideas on relationship to the living organisms emerged that differentially influenced each ethnical group that inhabits the different regions of the world. In other words, the various ethnical groups have their own way of interpreting their environment or their own world view [9].

The way people from the rural areas live and approach their natural resources is quite different from those living in the cities. However, both types of communities have in common that all live and benefit from these resources [9].

The bond formed between human beings and natural resources has caused, in many regions, an abuse in the way the biodiversity is used. The inadequate use of biodiversity has affected the vital cycles and the ecological relationships of many living organisms that depend one from each other [1]. The industrialization that emerged in the late eighteenth Century caused a deep change, not only in the way in which the relationship between humans and their natural resources takes place, but also in the form that natural capital is seen, which since then started to be comparable to the financial capital and infrastructure [10].

Within the industrialization development, people behavior dramatically changed, because it not only brought benefits and comfort, but also a striking economic inequality, creating very poor social groups with a profound imbalance in terms of rights, goods, and services. In addition, it caused different kind of pollution; change in the land use; and lack of care of the natural habitats, among other things. All of these problems have caused the global warming, which is modifying and destroying the world's biodiversity [1].

The big change regarding the way natural resources are seen by people and politicians, as well as, the policies for protecting them began in the 90s, when as a result of the change in the international markets, the growth of global economy and the political and social reorganization in some countries (mainly in Europe), a social growth occurred, not only in terms of the number of individuals, but also in the way such resources were used and distributed. However, history has shown us that such a change has not taken place along with the economic development. For instance, many human communities that are living in the Natural Protected Areas (NPA), from which most of the natural resources are obtained, still live in very limited and deficient conditions, compared to those who live in the cities, where a high percentage of the environmental services available are consumed [1].

Over the last decades, politicians have proposed the creation of "green" political parties and organizations, in order to solve the environmental issues that were being considered since the 70s. The first global conference regarding the environment, known as the "Stockholm Conference" in 1972, set the tone for the modification and redirection of environmental policies worldwide [1]. Nonetheless, the attending of these issues is a matter of national security and it must have an important place in each country's development plan [10].

In the late 70s, John Harshberger proposed the concept of "Ethnobotany," as a discipline that aims to analyze the interrelation between human societies and plant communities in terms of both environmental and sociocultural aspects [11].

This discipline considers, since its inception, the close relation between human beings and plants, not only as a simple compilation and description of plant species uses, but for understanding their changes due to domestication and evolution processes, as a result of their interaction with human beings. Also within the framework of Ethnobotany, many studies are carried out, in order to find and propose diverse strategies for sustainable use of plants in their natural environments.

Since the emerging of Ethnobotany in Mexico, many authors have contributed to improve and develop this important discipline. In particular, Efraín Hernández Xolocotzi concluded that the human–plant interrelation is determined by two factors: (a) the environment (the ecological conditions) and (b) the culture. By studying such factors in a time range, he was able to recognize that there are qualitative and quantitative changes in the used plants. Thus, the environment changes because of modifications in its components and by the action of man, while the culture changes due to the accumulation, and sometimes the loss, of human knowledge [12].

Likewise, Toledo et al. [13] suggested that Ethnobotanical work attempts to integrate those issues that usually are disintegrated. In other words, it integrates the botanical science to other disciplines, by a multicultural and multilinguistic approach, in order to answer the current social crisis with a truly committed science.

More recently, within the framework of Ethnobotany, many studies have contributed to the understanding of the man–plant relationship [14], which have shown that the traditional knowledge of the native people that inhabit the NPA, or any other relevant regions, is essential to detect the important species from the economic point of view and to define the minimum surface needed for their conservation.

It is not casuistic that, as Harmon [15] pointed out, at a planetary scale, human being diversity is closely associated to the main existing biodiversity concentrations. Indeed, this fact is the main reason for the overlapping between the areas with greater biological richness and those with high linguistic diversity. This overlapping is the best indicator for distinguishing a culture. Therefore, if biodiversity is endangered, cultural diversity is also so; this is precisely what Nietschmann [13] named "*symbiotic conservation*", concept that accounts for the mutual dependence of both types of diversity [13].

Domestication is not an instantaneous event by which wild plant populations are suddenly transformed in domesticated populations. It is an evolutionary process involving gradual changes in the relationship "plant–human being" by which a certain degree of interdependency occurs, in parallel to the effects caused by the artificial selection undertaken by human beings [16–18]. As a result of this selection, when domesticated plants are compared to their wild representatives, the former ones show morphological modifications in their useful parts, life cycle and genetic diversity and structure [19]. Some of these changes are not unidirectional or do not follow the same direction, because they are influenced by the biology of each species and the culture of the human beings involved in the domestication [18].

The diverse ethnobotanical studies undertaken have enabled to estimate that in Mexico there are between 5000 and 7000 useful plant species [20–22]. In particular, in the Tehuacán-Cuicatlán Valley, there are 1608 useful plant species recorded, from which 610 have at least one management type other than simple gathering [23, 24]. Among these managed plant species there are some annual weeds that grow spontaneously in cultivated fields, roads, or in home gardens [25–28]. Some others are perennials, particularly columnar Cactaceae in which it is possible to differentiate wild populations from those that are either morphological or genetically different due to their management [14, 29–39, 41].

It is worthy to mention the project entitled "Strategies for ex-situ conservation and propagation of useful plant species in the Tehuacán Cuicatlán Biosphere Reserve", which was carried out in the community of San Rafael Coxcatlán, Puebla, Mexico (Fig. 20.1), as part of the collaboration between FES Iztacala UNAM and Millennium Seed Bank of the Royal Botanical Gardens of Kew [14, 23–27, 29–45].

In San Rafael Coxcatlán, a total of 368 useful species have been recorded [46] and the community has made efforts to conserve all of them by propagating them in a greenhouse and in some specific locations. For doing so, 29 workshops were performed in which kids, adults, and young people from the communities (957 people in total) participated. In these workshops, 11,688 plants of 19 plant species (11,007 by seed and 681 by vegetative means) were propagated. A total of 2602 plant individuals (2462 derived from seeds and 147 from vegetative propagation) were successfully established and now are growing in the greenhouse of San Rafael Coxcatlán.

In relationship to the active components of the useful species, a research on plant physiology and phytochemistry was also carried out. A series of studies have been done regarding the content of secondary chemical compounds found in *Gymnosperma glutinosum* (Asteraceae), *Lippia graveolens* (Verbenaceae), and *Castela tortuosa* (Simaroubaceae), as well as about the seed aging deterioration of several species of Cactaceae. In addition, phytochemical studies have been done to evaluate therapeutic properties attributed to diverse plant species. The results obtained from these studies show that some of these species have antibacterial, antifungal, and antioxidant properties (Fig. 20.2).

In situ Conservation

Such an important place as the Tehuacán-Cuicatlán Valley, where their diversity and endemism rates are high, and so is the number of useful plants, deserves a well-planned conservation program including *in situ* and *ex situ conservation* actions. The former are those related to the "conservation activities that are undertaken in the natural habitat of organisms." It includes the protection of endangered species

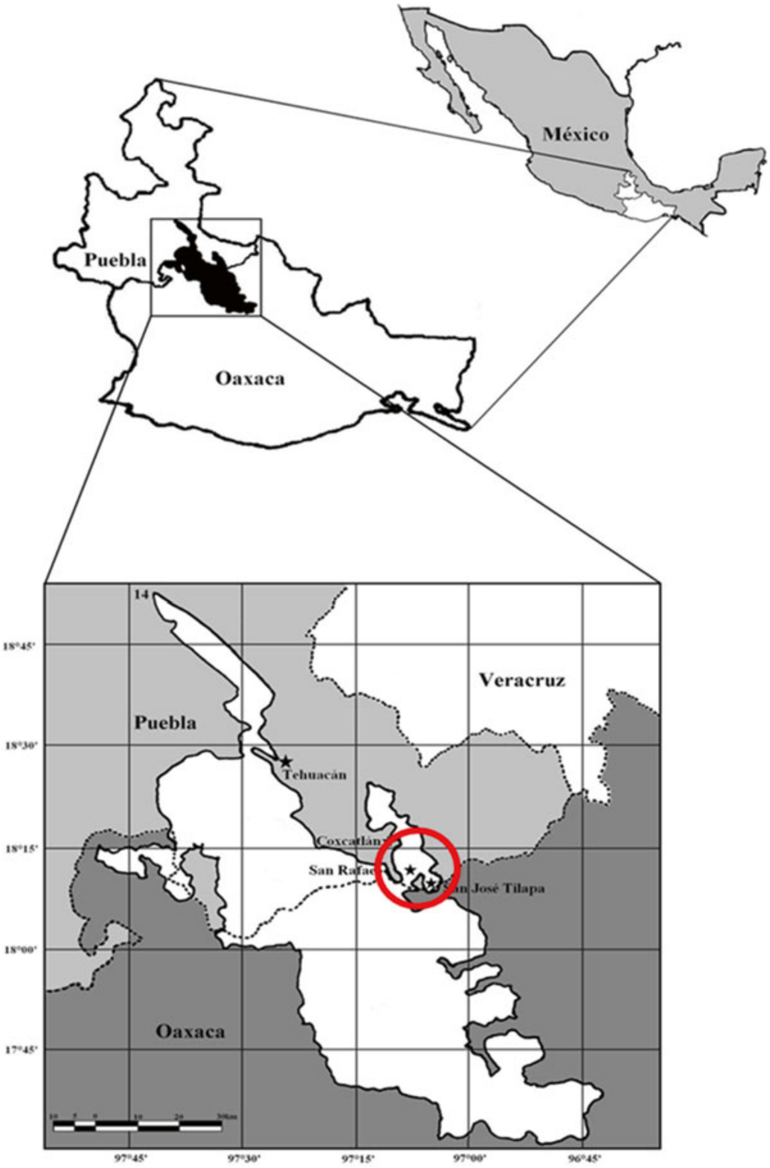
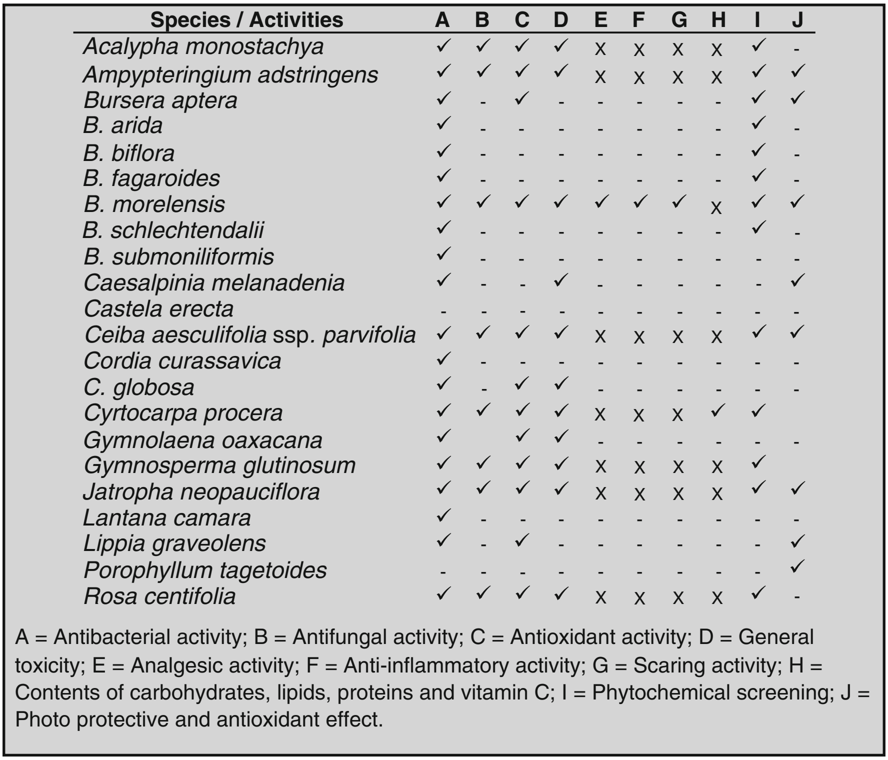


Fig. 20.1 Community of San Rafael Coxcatlán, Puebla, Mexico

and their habitats, as well as the biotic and abiotic interactions that take place between them [47].

In Mexico, the way to optimize the *in situ conservation* activities has been through the decree of NPA leaded by the National Commission for Natural Protected Areas of the Mexican Environmental Ministry (SEMARNAT, Secretaría de Medio



Species / Activities	A	B	C	D	E	F	G	H	I	J
Acalypha monostachya	✓	✓	✓	✓	x	x	x	x	✓	-
Ampypteringium adstringens	✓	✓	✓	✓	x	x	x	x	✓	✓
Bursera aptera	✓	-	✓	-	-	-	-	-	✓	✓
B. arida	✓	-	-	-	-	-	-	-	✓	-
B. biflora	✓	-	-	-	-	-	-	-	✓	-
B. fagaroides	✓	-	-	-	-	-	-	-	✓	-
B. morelensis	✓	✓	✓	✓	✓	✓	✓	x	✓	✓
B. schlechtendalii	✓	-	-	-	-	-	-	-	✓	-
B. submoniliformis	✓	-	-	-	-	-	-	-	-	-
Caesalpinia melanadenia	✓	-	-	✓	-	-	-	-	-	✓
Castela erecta	-	-	-	-	-	-	-	-	-	-
Ceiba aesculifolia ssp. *parvifolia*	✓	✓	✓	✓	x	x	x	x	✓	✓
Cordia curassavica	✓	-	-	-	-	-	-	-	-	-
C. globosa	✓	-	✓	✓	-	-	-	-	-	-
Cyrtocarpa procera	✓	✓	✓	✓	x	x	x	✓	✓	
Gymnolaena oaxacana	✓		✓	✓	-	-	-	-	-	-
Gymnosperma glutinosum	✓	✓	✓	✓	x	x	x	x	✓	
Jatropha neopauciflora	✓	✓	✓	✓	x	x	x	x	✓	✓
Lantana camara	✓	-	-	-	-	-	-	-	-	-
Lippia graveolens	✓	-	✓	-	-	-	-	-	-	✓
Porophyllum tagetoides	-	-	-	-	-	-	-	-	-	✓
Rosa centifolia	✓	✓	✓	✓	x	x	x	x	✓	-

A = Antibacterial activity; B = Antifungal activity; C = Antioxidant activity; D = General toxicity; E = Analgesic activity; F = Anti-inflammatory activity; G = Scaring activity; H = Contents of carbohydrates, lipids, proteins and vitamin C; I = Phytochemical screening; J = Photo protective and antioxidant effect.

Fig. 20.2 Species considered by local people as being of high conservation priority

Ambiente y Recursos Naturales). Despite the fact that the NPAs represent the best current option for conserving and protecting the natural capital and the services it provides, the current coverture on the national territory for such areas is still insufficient, for they barely represent 9.85 % of the whole territory [48]. Once the NPAs are decreed, it is necessary to develop a conservation and management program that integrates and sets actions to be carried out in short, medium, and long terms [47].

Even when *in situ conservation* is an excellent strategy, the main problems associated to the NPA decree indicate that after being appointed as such, they must be well protected against intrusions or anthropic destruction, which is difficult and expensive. Besides, the size of the NPA must be determined for each protected species, examining the population density in natural situations, for they must be large enough to maintain an adequate number of individuals of the species under protection. This situation is important, due to the fact that the population size of the species protected in these areas must gather the minimal genetic variability needed to survive. By doing so, these populations may be able to continue evolving in time. The ANPs decree brings serious social, political and even economic problems, because they limit the economic activities that were formerly done.

Accordingly, in Mexico, there is still much to be done regarding *in situ conservation*; the State has a big task in terms of promoting and generating strategies whose main and final objective is the conservation of the natural capital.

A particular case that deserves a special attention in this matter is the decree of the Tehuacán-Cuicatlán NPA, which is considered a very important reserve in Mexico. With approximately, 10,000 Km^2, the region bears almost 3000 species of vascular plants, from which 365 are endemic and 1608 are useful species.

Ex situ Conservation

Given the problems and challenges of *in situ conservation* and complementing its efforts, the *ex situ conservation* actions are also important for conserving and protecting our natural capital. They include those actions undertaken outside the natural habitat of the organisms. All these actions are mentioned in the ninth article of the Biological Diversity Convention and in the eighth objective of the Global Strategy for Plant Conservation [49].

The last 50 years have witnessed an unprecedented evolution of our knowledge on conservation and its interrelations with the goal of achieving sustainable development. Given the fact that world biodiversity is quickly diminishing; immediate conservation actions are required in order to safeguard many of the species that are currently disappearing [50].

Ex situ conservation consists in the maintenance of some biodiversity components outside its natural habitats, which includes, storing genetic resources in genebanks, as well as establishing field collections and managing species in captivity. The main objective of the *ex situ conservation* is to ensure the survival of the species and it must be considered complementary to *in situ* conservation, especially when working with critically endangered species [51].

Accordingly, *Ex situ conservation* aims to preserve taxa outside of their natural habitat, through different methods:

- *Gene and seed banks*, including germplasm, sperm, and egg cells banks.
- *Collections of In vitro,* including plant tissues and microbial cultures.
- *Reproduction of animals in captivity and artificial propagation of plants*, including the possibility, at least in some cases, of their reintroduction to their natural habitats.
- *Recollection of confined living organisms*, including zoos, aquariums and botanical gardens for research, education, and public awareness.

A key factor for biodiversity conservation is the genetic resources, defined as a material consisting of genes, proteins and metabolites or crude fragments of plants, animals or microorganisms of intrinsic or utilitarian value (actual or potential), which represent a fundamental characteristic of biocomplexity and therefore are part of the cultural and technological heritage of mankind [52]. Particularly, the plant genetic resources that have or might have any anthropocentric value are a product of its evolution, but also are useful for the improvement of genetic engineering [53].

The importance of plant genetic resources in Mexico can be seen, when it is realized that there are 50 native and 179 introduced taxa in the country that produces about 73–119 millions of pesos every year [53]. Nevertheless, all the species that are used and are sold locally, are not included and there is no way that we can have a real estimation of their economic input.

The expression “genetic resources” often replaces the concept of germplasm by referring to a group of species or genera (plant genetic resources, microbial genetic resources, etc.) that offer an economic or environmental utility. However, strictly speaking, the term germplasm is formed by the etymological root *germ* (beginning or inception) and *plasm* (formation). Thus, the term germplasm can be used for naming any genetic material that can regenerate a life form that is equal or similar to the original [53]. The centers responsible for the conservation of biodiversity contained in the germplasm are often called germplasm banks or *Seed banks*.

From the moment that human societies developed agriculture, the conservation of seeds became a necessary activity to maintain the cycles of recollection and sow, as well as to preserve contemporary plant diversity [50]. Consequently, the idea of preserving seeds of different plant species from all around the world in special places for guaranteeing their long-term viability, emerged at the beginning of the twentieth century. This idea highlights the proposal of the Russian scientist Nicolai Ivanovitch Vavilov [54], who aimed to increase the germplasm supplies of those species recognized for food or industrial uses, but also to improve the genetic material, at the time Russia was a very poor country. In order to achieve this goal, in almost 30 years Russians created and ordered huge biological collections which enabled them to preserve ex situ plant germplasm in a systematic way and defining some of the basic procedures for seed preservation [50].

The techniques to manipulate genes are developing and improving all the time. However, we are still unable to create them. Consequently, if a plant species with a unique genetic character disappears, there is no way of recovering it. This is the reason why millions of dollars are invested on seed banks, which represent one of the most important strategies of *ex situ conservation*. In fact, in some countries, germplasm banks specialized in the conservation of wild plants have a key role in the biodiversity conservation policies. In fact, each time it is more frequent that the technicians and researchers of the *ex situ conservation* centers actively participate in the design, development, and execution of *in situ conservation* programs [8, 50].

The presence of botanical gardens and seed banks stimulates and strengthens the implementation of strategies on those zones where conservation species concern occur. This task and the generation of original scientific knowledge by the academic research institutions are helping to protect the ecosystems [52].

Although it is true that *ex situ conservation* is a very useful approach, it is important to point out that its main “inconvenience” lies on the amount of economic resources needed. Nevertheless, in Mexico thanks to the efforts of the UNAM, the Millenium Seed Bank of the Royal Botanical Gardens of Kew and the CONABIO, the seed bank for wild species of Mexico exists formally since 12 years FESI-

UNAM Seedbank (BSFESI-UNAM), Registration: MEX-FLO-150-0903. This seed bank is a reservoir for the long-term conservation of wild plant species of the arid and semiarid regions of Mexico. Currently, the BSFESI-UNAM stores over 3500 seed accessions that represent close to 1700 species belonging to 137 botanical families, including Asteraceae, Mimosaceae, Cactaceae, and Fabaceae, among many others.

The BSFESI-UNAM has an active collecting program for obtaining plant materials from new regions and, in some cases in previously visited locations, given the fact that although collections with a larger number of seeds are needed. The BSFESI-UNAM also continues to carry out efforts to collect seeds from endemic, restricted distribution, endangered or useful species. In addition, researchers are also interested in tree species, as well as those related to domesticated plants. The work done in the Seedbank is also related to the development of diverse research activities that aim to identify, conserve and adequately use our flora.

Since our point of view, *ex situ conservation* is an excellent choice to protect many species without the need of large areas of land. In this sense, the seed banks allow the possibility of storing a great number of species for very specific purposes. For instance, in the case of the conservation of wild useful plant species, not only the plant germplasm is protected but also the ethnobotanical information associated to the collections, which is the starting point for carrying out studies about very specific subjects regarding the close man–plant relationship.

In the different research laboratories associated to BSFESI-UNAM, several research efforts have been implemented, in order to understand the interactions between people and plants, ethnofloristic richness, the relative importance of useful plant species richness in relation to general plant species richness, and plant management in the Tehuacán–Cuicatlán Valley of central Mexico (VTC). These studies recorded a total of 1605 useful vascular plant species (61.2 % of the total species richness of the regional vascular flora), this being the region with the highest absolute richness of useful plant species in Mexico recorded [24].

Also there have been studies, in order to document the floristic composition, richness, diversity, and traditional knowledge of the weeds growing in the cornfields of San Rafael, Municipality of Coxcatlán, Puebla. For that purpose, twelve cornfields were sampled using Canfield's lines, and 20 farmers were interviewed, whom ages fluctuate between 32 and 80 years. A total of 43 species of 12 families of vascular plants were recorded. From them, farmers were able to recognize between 20 and 31 plant species and there was not a significant correlation between farmer's age and the number of identified species. Only 11 species were recognized as useful, and there were not evidences of manipulation in any of them [25].

In San Rafael Coxcatlán, a total of 368 useful species have been recorded [46], from which the seeds of 134 were stored in the FESI Seed Bank, including 17 that are considered by local people as being of high conservation priority (Fig. 20.2).

The stored seeds from the 134 species belong mainly to the following plant families: Asteraceae, Mimosaceae, Euphorbiaceae, Solanaceae, among others (Fig. 20.3).

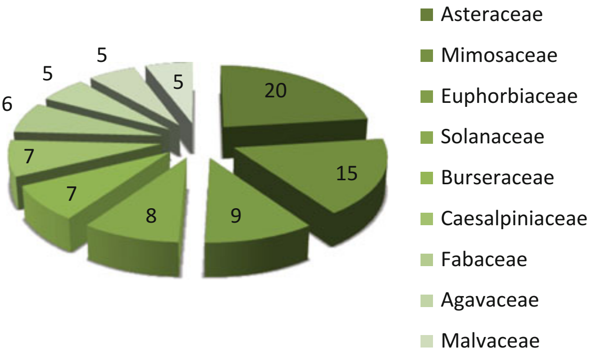


Fig. 20.3 Dominant plant families among the useful plants conserved in the seed bank

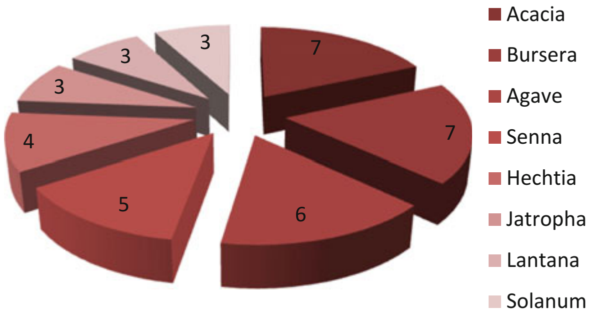


Fig. 20.4 Dominant genera among the useful plants conserved in the seed bank

The most common genera in the seed bank are *Acacia*, *Bursera*, *Agave*, *Senna*, among others (Fig. 20.4).

In addition, from the seed collections of useful plant species stored in BSFESI-UNAM, various studies regarding the therapeutic properties of some useful wild plant species from Mexico have been done. Once the uses of plants are identified in any area, then it is possible to select some plants species, in order to recognize and correlate their phytochemical features and their therapeutic consequences. Accordingly, such studies have been implemented on the basis of the ethnobotanical knowledge of the VTC and by using the germplasm stored in the seed bank. The species that have been so far studied are *Lippia graveolens* [55], *Cordia curassavica* [56], *Gymnosperma glutinosum* [57], *Acalypha monostachya* [58], *Bursera morelensis* [59], *Buddleja perfoliata* and *B. scordioides*, and *Yucca* [45].

In summary, the biodiversity inventory, the generation of information regarding its distribution, uses, ecological and environmental requirements, and phytochemical features are the basic platform that we need to have, in order to be able to propose their sustainable management for ensuring their protection and conservation. Accordingly, all the germplasm stored in the seed banks represents the raw material for doing so. In particular, the bond between the ethnobotanical studies and the seed banks should always be strong, in order to generate the information of our useful plants.

The educational and *ex situ conservation* activities undertaken in San Rafael Coxcatlán located in the Tehacán-Cuicatlán NPA, is an example of a sustainable management project that enables the protection of the natural capital and the benefit of the people, within the framework of the activities leaded by a seed bank.

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Chapter 21
Biosafety and Environmental Releases of GM Crops in Mesoamerica: Context Does Matter

Francisca Acevedo, Elleli Huerta, and Caroline Burgeff

Abstract Since the use of products from modern biotechnology entails potential risks and possible adverse effects to human health and the environment, it is only reasonable to pursue that its use is done under responsible biosafety frameworks.

Context is an indispensable consideration for biosafety practices. Mesoamerica is an important Megadiverse region, a Vavilov center of origin and genetic diversity of a diverse range of economically relevant crops fundamental to humankind. Nevertheless, baseline data obtained locally hardly exists so as to be able to set out the important questions in relation to the technology that is being promoted to be used. It cannot be assumed that potential risks can be analyzed in an abstract and generic receiving environment and translated to any one new setting and expect it to "act accordingly."

The in situ conservation of the genetic diversity of local landraces and wild relatives is fundamental to maintain the continuously evolving genetic capital of a crop, which is a source to respond to possible productive challenges. We elaborate on two approaches to consider biosafety and protection aspects in Mexico, given its context: the establishment of biosafety levels to be considered during risk analysis, and protection frames.

Keywords Biosafety • In situ conservation • Wild relatives • Risk analysis

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Biosafety in Context

Modern biotechnology (as defined by the Cartagena Protocol[1]) is a technology that has resolved important problems and has brought benefits to humankind, for example in medical applications, and is seen by many as a potential tool to face, and possibly resolve, future challenges in food production [1]. Environmental releases of Genetically Modified (GM) crops have increased in the last decades and 175.2 million hectares of this kind of crops had been cultivated worldwide in 2013; 90 % of this surface is distributed mainly in five countries [2]. The potential risks and possible adverse effects to human health and the environment derived from the use of products from modern biotechnology are a matter of concern in biosafety. The term "biosafety" in this chapter relates to the idea of the "safe and responsible use of modern biotechnology."

Under this definition, biosafety neither pretends stopping the use of modern biotechnology, nor promoting its use; it really entails "making sure that if it is used, doing so in the most safe and responsible way possible." In order to identify and evaluate the possible adverse effects of genetically modified organisms (GMO, products of modern biotechnology) on the environment, including biological diversity[2] case by case risk assessments should be made, in which the receptor organism of the genetic modification, the genetic construct inserted in it, and the receiving environment should be considered in the assessment.

There certainly are cases where the most responsible thing to do is not to use modern biotechnology at all, most likely in those cases where unresolvable uncertainty prevails or where risks (and therefore probable consequences if the risks do occur and effects follow) are superior to the possible benefits that a given "transformation event" (i.e., a GMO is produced) may offer. Modern biotechnology is one of many options available to counter with unresolved problems. No need to say that care must be taken in studying and analyzing which option is the most advisable to use in each problem solution seekage, so that a given solution isn't a new problem generator.

From a responsible standpoint, we could say that, given that technology always conveys risks (i.e., no zero risk), it is only advisable to take the risk/s when other possible options/solutions to a given problem are inexistent or would be too time consuming or resources needy otherwise unbearable.

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[1] Article 3 (i) of the Cartagena Protocol defines Modern Biotechnology as "the application of":

(a) In vitro nucleic acid techniques, including recombinant deoxyribonucleic acid (DNA) and direct injection of nucleic acid into cells or organelles, or
(b) Fusion of cells beyond the taxonomic family, that overcome natural physiological reproductive or recombination barriers and that are not techniques used in traditional breeding and selection

[2] Case by case, as referred to by annex III article 6 of the Cartagena Protocol (Secretariat of the Convention on Biological Diversity (2000)).

Mesoamerican Context

Mesoamerica is an important Megadiverse region of the world, from a biological as well as from a cultural point of view; it is Vavilov center of origin and center of genetic diversity (COCGD) of a diverse range of economically relevant crops fundamental for humankind food supply [3, 4]. It is also considered a "biodiversity hotspot" where important concentrations of endemic species are losing their habitat in an exceptional way [5]. Context is then vulnerable and complex deriving from, among others, contrasting geographical, biological and environmental settings, as well as from diverse human activities such as multiple agriculture management systems existing at once.

From a regional (i.e., Mesoamerica) point of view, making sure that modern biotechnology is used responsibly and in the safest way possible is a challenging task. In most cases, context, i.e., the biological, environmental, social, economic, socioeconomic realities, and diverse agricultural practices, is unknown, or barely known to say the least. Baseline data hardly exists so as to be able to set out the "what's," the "where's," and the "how's" in relation to the technology that is being promoted to be used (regarding the qualifying and quantifying of the effects or impacts of the use of this technology in the environment). Mesoamerica, being a COCGD, implies that its context is not only not known enough but complex, nevertheless it mustn't be eluded, oversimplified, overlooked or not accounted for in relation to the quest of solving the identified problems.

How Far Is Extrapolating Data Possible?

Although the principle of the case by case risk assessment for the environmental release of GM crops implies that the receiving environment is a fundamental part of the equation, the easiest way forward, supported by some, would be to assume that what we know (from data to analysis) from the experiences gained in other parts of the world, mostly from domesticated crops cultivated in modern intensive type agricultural settings, could be extrapolated to any other context. While some of the data might be extrapolated (as is argued in García-Alonso et al.) [6], there is a whole set of data, information, and knowledge that needs to be developed "locally" … no other way about it!

The feasibility of extrapolating data under the argument of it being useful and mostly sufficient has been central of those who state that using modern biotechnology has no "new risks" other than the usual ones coming from "known agricultural practice," also arguing that if no real damage has appeared when using X or Y GMO elsewhere, they see no reason to believe it would appear elsewhere (damage).

But context does matter. It cannot be assumed that potential risks can be analyzed in an abstract and generic setting/context/receiving environment and translated to any one new setting and expect it to “act accordingly” … this is too simplistic. These experiences certainly are of value, but the information behind them could hardly help us understand the potential risks we confront in a region such as Mesoamerica. Aspects, issues, and factors are all too different to expect similar risks, effects, and consequences altogether.

What is known in relation to the biology of domesticated crops mostly comes from studies done on the crops in highly controlled agricultural settings, generally neither where the crop was domesticated, nor where genetic diversity thrives nowadays. This is the case, for example, of *Gossypium hirsutum* (the cotton species most cultivated worldwide), which originated in Mexico and where both tetraploid (*G. hirsutum* and *G. barbadense*) and diploid (*G. aridum, G. armourianum, G. davidsonii, G. gossypioides, G. harknessii, G. laxum, G. lobatum, G. schwendimanii, G. thurberi, G. trilobum,* and *G. turneri*) wild species exist but for which most of the published scientific literature is based on data arising from the cultivated crop and far away from its natural context [7–9].

What we knew till recently, in relation to the biology of the *G. hirsutum* species in the natural settings in its center of origin and genetic diversity in Mexico, was limited. It is only now, after many years of research that we are starting to learn about the distribution, biology, ecology, and genetics of wild cotton, including its wild relatives [8, 10].

Crops Originating in Mesoamerica

Crops such as maize, beans, squashes, tomatoes, vanilla, chilis, among others, including their wild relatives[3] are commonly present here, in agricultural and natural environments, many of which are considered to be under domestication continuing to exchange genetic material through gene flow, both naturally and facilitated by farmers through nearness of the cultivars with their wild relatives (Fig. 21.1) [11–13]. The in situ conservation of the genetic diversity of local landraces and wild relatives is fundamental to maintain the continuously evolving genetic capital of a crop, which can become a source to respond, for example, to possible productive collapses derived from abiotic or biotic stresses.

The geographical distribution of a species, in this case, the crop’s wild populations and its wild relatives, tells us about its geographical, climatic, and ecological preferences. Habitats are sometimes shared between crops and their wild relatives, and if your goal is to conserve the gene pool,[4] you must also target the habitats where they prosper.

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[3] Source of the plasticity present in these crops.

[4] “Genepool: The sum total of genes, with all their variations, possessed by a particular species at a particular time” (GapAnalysis 2014, at http://gisweb.ciat.cgiar.org/GapAnalysis/?page_id=149&langswitch_lang=en#letter_g).

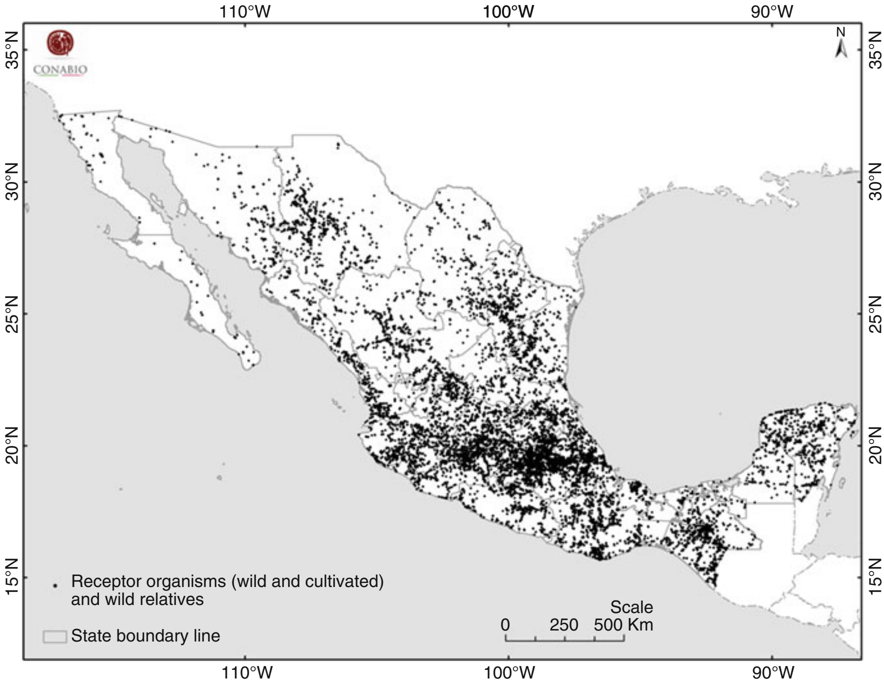

Fig. 21.1 Records in CONABIO databases of receptor organisms and wild relatives of GM crops released at least once in the Mexican territory (these include maize, wheat, potato, tomato, rice, tobacco, banana, alfalfa, pineapple, flax, cotton, canola, chili, papaya, safflower, lemon, melon, pumpkin, and carnation)

The Mesoamerican region is unique. It is COCGD of a variety of economically important crops, most of the wild relatives are present in its territory and some agricultural practices even promote genetic exchange between them. The types of agricultural practices are diverse, ranging from the more traditional practices in rural rainfed lands to the more technified type agriculture in the irrigated areas. People's customs and traditions are also different, translating into different cultural values and common day practices. The kinds of aspects that must be taken into consideration in one context are different from those that must be taken into consideration in a different context.

In the next sections of this text, we elaborate on two approaches to consider biosafety and protection aspects in Mexico, a Mesoamerican country, given its context. One implies the establishment of biosafety levels to be considered during risk analysis, and the other consists of protection frames legally established in the National Biosafety Law [14].

Biosafety Levels

After years of analyzing the potential risks in relation to the possible release of GMO into the environment, the National Coordination of the National Commission on the Knowledge and Use of Biodiversity (CONABIO) has developed the use of a set of "biosafety levels" that are meant to be indicative of the level of overall risk plausible in relation to the use of GMOs in the environment and the management of that given level of risk under the context of regions which are center of origin and genetic diversity of crops [15]. Three possible biosafety levels (I, II, and III) are described, in which each GMO can then be classified according to some simple predefined rules, including if the species in which the genetic construct was inserted has its center of origin in the region and if genetic diversity centers are present. Depending on the level assigned to a GMO, the minimum necessary requisites that must be met to then ponder releasing it into the environment, including the capacity of managing the identified risks, both of the proponent as well as of the competent authorities responsible of the issuance of the permits. These levels are:

Level I: A GMO developed from a species that has not originated in the region, and for which there are no centers of genetic diversity, i.e., no wild relatives nor landraces present (an example being soybeans for the Mesoamerican region). Minimum requirements at this level would be the warranty of (a) an adequate monitoring system in place with respect to the environmental effects originating from the release of the GMO, (b) putting into practice the necessary biosafety measures according to the characteristic expressed by the inserted genetic construct.

Level II: A GMO developed from a species which did not originate in the region but in which centers of genetic diversity are harbored/present. An example would be wheat, which originated in the Middle East but for which Mexico harbors a wild relative (*Aegilops cylindrica*) and landraces [16, 17]. Additional to the requirements in Level I, warranty would include (a) the existence of a genetic resources information system harboring/including the necessary data on the species that was used to originate the GMO, (b) installed capacity (both information and necessary tools) to detect the genetic constructs inserted in the particular GMO, so as to be able to (c) monitor systematically both the genetic resources as well as the eventual presence and/or introgression of a genetic construct in these resources including the possible effects and its consequences.

Level III: A GMO developed from a species which originated in the region and for which genetic diversity is present (wild relatives and/or native landraces). Examples would include beans, chiles, squashes, cotton, vanilla, maize, etc. For an GMO in this level, besides warranting considerations in I and II, additionally (a) the geographic location of the regions that contain the genetic diversity of the species from which the GMO was developed needs to be identified, (b) protection measures for the genetic diversity in these regions must be identified and put in place, and (c) the proponents of the technology and the competent authorities must make sure these areas will/would not be vulnerated either from activities related to the release of the GMO into the environment or other uses that could be given to the GMO (i.e., mobilization, contained use, use as food, industry, forage, etc.). For GMO at this level, it also becomes necessary to determine if local management capacity of the risks by local authorities, proponents, and users is in place and is sufficient.

A biosafety management system based on implementing biosafety levels in centers of origin and of genetic diversity would allow an efficient process that would seek to warrant an adequate management of the associated risks of a GMO release into the environment (this system does not substitute in any way a case by case risk assessment). Such a system should be financed by the proponents of using modern biotechnology and implemented with the support of public research institutions.

Up to now, many releases have taken place in Mexico, the first applications being in 1989 [18]. Nevertheless, little is known about the possible consequences of such releases. Even though more than 22 different GM crops have at least been trialed in the fields,[5] the three most released GM crops up to know are GM soybean, GM cotton, and GM maize (levels I, III, and III, respectively, for the Mesoamerican region). Each one of them has particular issues that must be considered when accounting for the relevant issues [19].

Even though GM soybean enters into level I, certain problems have arisen mostly related to the technology package used (glyphosate to control weeds in the agricultural area). Lately, its pollen is being found in apiculture production that is exported to buyers that are now reluctant to consuming such honey (which again could in turn affect honey production scales in the mid and long term, and have its effects at the ecosystem level due to a possible reduction in honey production activities indirectly affecting native vegetation).

In the case of GM cotton (level III), the fact is that recombinant proteins expressed from genetic constructs of GM cotton events have been detected in at least half the wild tetraploid cotton metapopulations present in Mexico [9]. The possible sources and routes by which the genetic constructs might have arrived are unknown, this is also true in relation to the effects and consequences they might represent, targeted research is underway. Up to now, neither the proponents nor the competent authorities have openly reacted to the findings [9] or to the warnings made by some scientific institutions (such as CONABIO has in its risk assessments).

GM Maize (level III) has been released in Mexico in two time periods, during the 90s for four consecutive years (1995–1999) and later on starting 2009 once the Biosafety Law and its regulation were already in place; both proponents and competent authorities somehow felt at ease once the minimum proper legal framework was in place and somehow being implemented (Fig. 21.2). Up to now, commercial releases have not taken place in Mexico even if applications exist in the Federal Government, while Honduras, also richly diverse, has already undergone such step forward (see at http://bch.cbd.int/database/record.shtml?documentid=105078).

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[5] 4281 case by case risk assessments have been performed by CONABIO since 2000 as a support for decision making of the Federal Government.

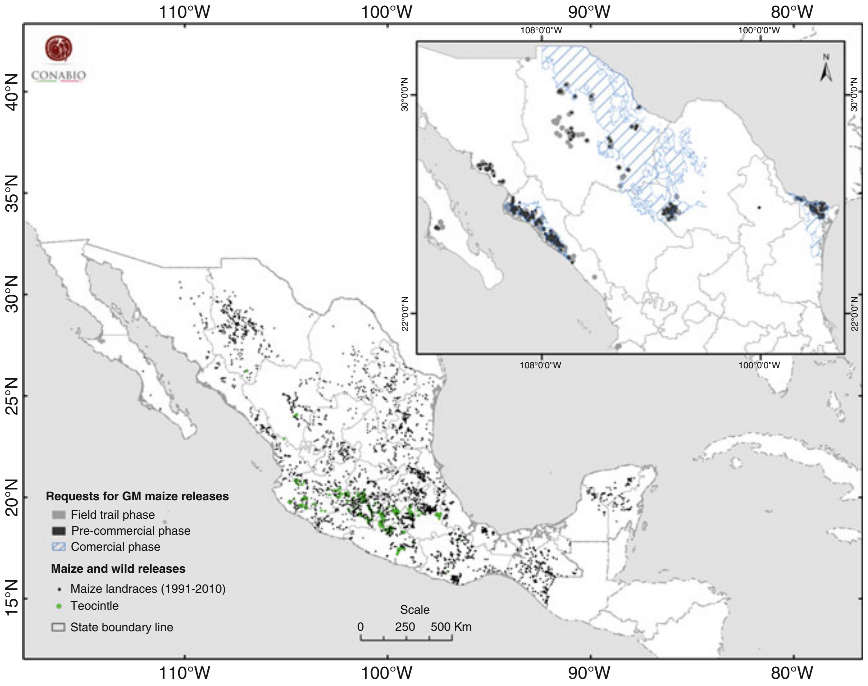

Fig. 21.2 Distribution of maize landraces records from 1991 to 2010, as well as the historical registers of teocintle, its wild relative. The in box shows GM maize release applications in Mexico (not all applications have been released, commercial scale releases have been applied for but not resolved yet)

We can foresee that such releases will be a source of constant flow of genetic constructs towards the native maize landraces present, as well as towards some of its wild relatives too. Some of the big questions in the case of maize in its Mesoamerican context are: "how will the genetic constructs present in the GM maize being released at a commercial scale become part of the native genetic diversity present?", and then, "what possible effects and consequences might this bring?", "will this be reversible"? (probably not!), "who might it affect in the short/medium/long term?" These kind of questions and many others arise, especially considering that maize is the staple food for the region (daily maize intake per person in Mexico is considered to be around 350 g[6]) and it is one of the three most cultivated and consumed cereals in the world [20, 21].

Unfortunately, not all involved actors seem to be aware of these issues. Proponents, mostly represented by the big multinational seed companies (although some public research developments have been trialed already and/or are in development), do not seem to be puzzled by the problematic. Most proponents have not done a real effort for learning from the releases made in the period (1989–2014)

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[6] Mostly in an almost unprocessed way.

in relation to the midterm possible effects in the environment. The target seems to be to "advance" through using new techniques, assuming that these are the answers to all the problems related to agriculture and food production, obviating the "receiving environment" aspects to be considered in risk assessment. What puzzles at the end of the day is the absence of wonder by proponents of modern biotechnology as to what could possibly occur in a medium or long term frame in the above described context, it seems not to be an issue worth pondering about. But, genetic diversity is key to future answers to unknown or unresolved problems, why put it at risk? Is this a responsible way forward?

Legal Protection Frames

The Mexican biosafety law, even though not well seen by many detractors of the use of modern biotechnology, does have several clauses in place so as to trying to restrict GMO releases into the environment when these may affect the diversity present in the center of origin and genetic diversity of diverse crops, among other issues. Among these are (a) the determination of centers of origin and genetic diversity of crops; (b) GMO free zones; and (c) Natural Protected Areas (ANP in spanish).

What is straightforward are the ANP, GMO cannot be released in these areas, although there is an exemption. Such is the case of using GMO in case of "bioremediation" but only in the external "buffer zones," that is, excluding the "nuclear zones" of the ANP.

On the other hand, GMO free zones have never been declared yet, nevertheless things are starting to move because some applications for free zones already exist and the Federal Government must put the necessary regulation in place in order to fulfill demands. GMO free zones have to do with coexistence issues [19] and possible effects of GMO activities to organic processes and/or its products as well as to biodiversity on a whole. It is definitely not an easy issue. One of the first applications has to do with GM soybeans in Yucatan and honey production (principally exported to Europe).

Lastly, determining "centers of origin and genetic diversity" (COCGD) results challenging but an interesting tool in relation to biosafety issues on a whole. What the Biosafety Law calls for is determining these COCGD (see Box 1 for technical definitions), both the species and the areas that contain them so as to protect them from possible effects from the release of GMO into the environment. This has to

Box 1: A Conceptual Framework for Conservation and Biosafety at Mesoamerican Crop Centers of Origin and Domestication

Valeria Alavés and Ana Wegier

Diverse fields of knowledge, such as botany, geology, archeology, genetics and evolution, have explored fundamental questions about where, when, and how crops were domesticated. Most studies revolve around notions regarding centers of origin, domestication, and genetic diversity of cultivated plant species; however, the use of these concepts is very heterogeneous in literature because, to some extent, they drag historical discussions that arose when limited evidence was available and also because they were mainly formulated with examples coming from few model crops, which made these concepts unsuitable for some cultivated plants, like those domesticated in Mesoamerica.

In order to homogenize the common conceptual framework about the domestication process in Mesoamerica and to consequently be able to implement relevant conservation measures and biosecurity strategies, a workshop that reunited more than 40 researchers and specialists from several Mexican and International Institutions was held (Wegier et al., 2012).[7]

Four main categories conformed the topics for discussion in the workshop: (1) concepts of center of origin and domestication; (2) evidence used in the characterization of centers of origin and domestication; (3) characteristics of the processes of origin and domestication; and (4) difficulties in the determination of centers of origin and domestication. As a final product, concepts of center of origin, domestication, and diversity were agreed and are presented below.

When referring to domesticated plants, from a general standpoint, there are five types of "centers" or "areas" that are particularly relevant and represent different biological materials, phylogenetic stages, or evolutionary processes:

1. Phylogenetic center of origin of the wild progenitor: the area where the wild progenitor species originated, that will eventually be domesticated. The origin of a wild taxon results from evolutionary processes common to all biota (e.g., mutation, natural selection, genetic drift, hybridization) and does not imply human intervention. Thus, the area where this processes occur is of phylogenetic importance on an evolutionary time scale; however, it may or may not harbor, at present, the wild relatives of the crop species.
2. Center of origin of the wild progenitor: the current geographic and ecological distribution of the immediate wild progenitor species. This area is

(continued)

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[7] Wegier A, Alavez V, Jardón L y S. Petrone. Prueba superada: un marco conceptual para la conservación y bioseguridad en los centros de origen y domesticación mexicanos. Revista Oikos N. 5 Enero 2012, pp. 23–28.

Box 1 (continued)

essential from a conservation point of view and therefore must be separated from area (1) although they may or may not correspond. Both are subjected to the same evolutionary processes; however, this area corresponds to the actual region that can be protected today.

3. Center of diversity of the wild progenitor: a diversification area where outstanding levels of genetic and phenotypic (e.g., morphologic, physiologic, or ecologic) diversity are displayed by the wild progenitor species prior to domestication.
4. Center of domestication: is the bio-cultural area where the wild progenitor populations and those under artificial selection differentiate genotypic and phenotypically, that is, where the actual domestication process takes place. This region may contain those wild progenitor populations most closely related to extant domesticates, but in other cases the domestication process may occur away from the natural area of distribution of the wild progenitor populations, due to human transportation. The process is not necessarily punctual and may continue over a long time, begin several times and vary in intensity, depending on the degree of human intervention. As a consequence, domesticated plants can exhibit a wide range of differentiation from its wild progenitors as well as variable levels of dependency from human beings.
5. Center of diversity of the domesticate: the area(s) where the domesticated plant acquires genotypic and phenotypic diversity post-domestication under cultivation. The causes for the higher levels of crop variation are related to environmental, social, and cultural conditions that operate jointly, enhancing the process of differentiation in several domesticated forms. The diversification centers of domesticated plants are the areas where different domesticated forms are developed through the artificial selection of plant populations' variation. This selection is tightly related to the diversity of uses and management practices of human groups.

In conclusion, given that plant domestication is the evolutionary process of plant populations from which humans obtain satisfiers by selecting some phenotypes above others, the concepts of center of origin, center of domestication, and center of genetic diversity must reflect the dynamism in time and space of the evolutionary processes that underlay them. Thus, when discussing difficulties associated with the identification and designation of these areas, it is necessary to keep in mind the material being studied, conserved or regulated, and also the evidences needed to identify each area, especially for the process of domestication where a broad and

(continued)

Box 1 (continued)

diverse collection of data coming from different disciplines is necessary (e.g., morphometry, conservation genetics, linguistics, archaeobotany, history, ethnobotany, among others).

Of utmost importance are the wild, conspecific relatives as well as traditional landrace materials and, thus, their respective centers of distribution and diversity. The phenomenon of gene flow is the most important factor potentially making the identification of a center of domestication difficult but also the fact that in Mesoamerican domestication processes are characterized by being continuous and multiple (occurring in different areas).

be done for every species originated in Mexico, including their wild relatives, as these are part of the genetic pool.

Work was undergone in the case of maize triggered by external pressure as to release maize into the environment once the Biosafety Law was put in place [15, 22]. A very big effort lead by CONABIO, with financial support of the Competent Authorities (SEMARNAT[8] and SAGARPA[9]) as well as by CIBIOGEM,[10] took place so as to have the necessary elements to be able to determine these areas in Mexico. A huge team composed of nearly 300 people (more than 215 coming from nearly 70 diverse research institutions) worked together to provide the most recent and complete information related to maize and its wild relatives (see results in http://www.biodiversidad.gob.mx/genes/proyectoMaices.html). This information was provided for decisionmaking related to the areas and protection measures recalled by the Biosafety Law to be put in place by the competent authorities SAGARPA and SEMARNAT. See Box 2 for details.

Work has also been undergoing for other species including cotton, squashes, amaranth, vanilla, cempasúchil, chile, xoconostles, green tomatoes, and aguacate (http://www.biodiversidad.gob.mx/genes/centrosOrigen/proyectosCdeO.html). Two big projects are underway so as to have further elements regarding genetic diversity, squashes and beans.

Cotton should be next on the list in the determination of COCGD, and the necessary information has been gathered and is available for the competent authorities. This is a pressing issue taking into account the more than 15 years of GM cotton releases into the environment in Mexico, and the presence of recombinant proteins coming from commercial (and non commercially available) GM

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[8] SEMARNAT (Ministry of the Environment).

[9] SAGARPA (Ministry of Agriculture).

[10] CIBIOGEM (Intersecretarial Commission on Biosafety of GMO).

Box 2: Center of Origin and Centers of Genetic Diversity, Maize as a First Attempt

Laura Saad, Patricia Tovar, and Alejandra Barrios

Through the National Biosafety Law[11], the legislative power recognized the relevance of Mexico being the center of origin of diverse species, several of them of global importance.

This is reflected in the introduction of novel regulatory mechanisms in order to determine the "centers of origin and genetic diversity of species" (COCGD), as well as the establishment of restrictive rules to undertaking activities with genetically modified organisms (GMO) in such centers. It is in this manner that the protection of the species and the areas where they are present is reinforced, and the precautionary principle towards possible risks that could affect biological diversity is strengthened.

The agreement that determines the maize COCGD,[12] gives preference to the benefits, because the conservation of the species for which Mexico is custodian, constitutes a natural patrimony of common benefits not only to us Mexicans, but to the world, and even though its emission might imply costs in its compliance, the Mexican State must act responsibly, putting the common welfare above individual profits.

cotton constructs in four out of eight of the recently described metapopulations of wild tetraploid cotton (*Gossypium hirsutum*) present in the coasts of central and southern Mexico [9]. It is also a pressing issue to determine the COCGD of beans, taking into account a recent GM bean development by INIFAP,[13] a scientific research body of SAGARPA.

Conclusions

In the case of Mexico, some see the Biosafety Law as impeding their commercial development with modern biotechnology, others see it as a week and skew regulation that is in place to have interested sectors in using modern biotechnology be able to do so readily. What is certainly true is that this technology, as any other available

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[11] http://www.diputados.gob.mx/LeyesBiblio/pdf/LBOGM.pdf.

[12] Ministry of Environment and Natural Resources (SEMARNAT) 2011. "Manifestación de Impacto Regulatorio del Proyecto de Acuerdo por el que se Determinan los Centros de Origen y Diversidad Genética Del Maíz En Territorio Nacional. Contrato DGSPYRNR-No-002/2011". Editor: Saad Alvarado Laura. México, 2011. Published in: http://207.248.177.30/expediente/v99/_B001104104.pdf y http://207.248.177.30/regulaciones/scd_expediente_3.asp?ID=04/0851/171111.

[13] INIFAP, National Institute for Forestry, Agriculture and Livestock Research.

technology developed by humankind presents great promises and challenges, and it is our task to take the correct path forward, neither being dazzled by the expected outcomes and promised problem resolutions, nor by generically discarding its use. What is most important is to take into account the surrounding context. Modern biotechnology is a clear promise to solve particular problems, but regions as rich and diverse in biological and genetic resources should first identify what those national problems are, and analyze what the plausible solutions could be; modern biotechnology efforts should only be undergone when no other plausible solution exists, or when time and/or money are at odds of solving it correctly. At least in Mexico such an exercise has not really taken place, neither in the case of maize [23] nor for many other important agricultural crops for which Mexico is COCGD, and for which much could be at risk. Betting without doing this becomes a risky business considering what is at stake and the immense number of uncertainties still prevalent regarding the effects of using modern biotechnology.

Acknowledgements This text is the result of an accumulation of work undergone under the auspices of the National Commission of Knowledge and Use of Biodiversity (CONABIO) as well as to several fundings from GEF and SEMARNAT, as well as collaborations with diverse research institutions and the never ending support of the CARB. Maps were developed by Oswaldo Oliveros.

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Chapter 22
A Human Rights Perspective on the Plant Genetic Resources of Mesoamerica: Heritage, Plant Breeder's Rights, and Geographical Indications

Jorge Larson, Claudia Aguilar, Fabiola González, and Desirée Sánchez

Abstract The values of the plant genetic resources (PGR) described in the previous chapters are multiple and cannot be overstated. These biological resources and the heritage they represent are being dissected by science and technology, and by laws, both multilateral and national, and rights are being claimed over them at various levels and on different grounds, individually and collectively, privately and as public goods. The main argument in this contribution is that natural and cultural heritage, biological resources, and intellectual property are legal concepts that should be grounded deeply in a human rights perspective, in particular on economic, social and cultural rights. A legal perspective provides context to the complex innovation and appropriation strategies that are taking place, by industrially oriented life sciences and technologies, but also by small rural producers and their associations, by social movements, by public research institutions, and by municipalities, states and nation states. From seeds as public goods and heritage of mankind to registered plant varieties and patented genes, many things have changed over the last three decades in the regulation of PGR. For better or for worse, legal developments have taken place, and they have impact on the conservation, research, documentation, and use of biological and genetic resources. The more or less recent multilateral legal frameworks reviewed include two conventions on world heritage, a convention on biological diversity, a treaty on PGR for food and agriculture, a convention on industrial property, the intellectual property rights obligations of a multilateral trade agreement, and a union with a binding act on plant breeder's rights. In heritage, cultivated plants, plant breeder's rights and geographical indications, we provide a quantitative panorama for this region in which we consider all continental countries from Canada to Colombia in a comparative approach that provides a wider context that is useful in framing the issues at various levels. The fact that PGR are essential for the future of humankind is recognized by all. How to best

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keep them diverse, and available to communities, is another question. The role of formal "protection," "registration," or "documentation" as heritage, as national resources, or as private intellectual property rights in these processes has been in debate for decades. Beyond research or debate, things are happening in many areas, the enclosures of the mind advance, which may have long lasting biological, cultural, and socioeconomic effects. However, it is the outcomes of social and legal action, public and private, individual and collective, that will define what PGR are inherited to the next generations.

Keywords Human rights • Heritage • Biological resources • Intellectual property

The values of the plant genetic resources (PGR) described in the previous chapters are multiple and cannot be overstated. These biological resources and the heritage they represent are being dissected by science and technology, and by laws, both multilateral and national, and rights are being claimed on them at various levels and on different grounds, individually and collectively, privately and as public goods.

The main argument in this contribution is that the legal protection of natural and cultural heritage, biological resources and intellectual property is, or should be, grounded deeply in human rights [1], in particular on the economic, social and cultural (ESC) rights [2]. A legal perspective provides context to the innovation and appropriation strategies that are taking place, implemented by industrially oriented life sciences and technologies, but also by small rural producers and their associations, by social movements, by public research institutions, and by local governments and nation states.

From seeds as public goods and heritage of mankind to registered plant varieties and protected geographical indications, many things have changed over the last 20 years in the regulation of PGR. For better or for worse, legal developments have taken place in these areas and they may have impact on the human rights of rural, peasant and indigenous communities, on the conservation, research, documentation, and use of biological and genetic resources, as well as on the availability and quality of food in urban environments.

The multilateral legal frameworks reviewed, and whose main legal components are indicated in table format, include a covenant on ESC [2]; two conventions on world heritage [3, 4]; a convention on biological diversity (CBD) [5]; a treaty on PGR for food and agriculture [6]; a convention on industrial property [7]; a union with a binding act on plant breeder's rights [8]; and the intellectual property agreement of a multilateral trade organization that recognizes geographical indications [9].

The stakes are high and they are not new to the Mesoamerican region or to the debates on people, plants, and patents [10]. Domesticated plants are substantial to the cultural concept of Mesoamerica, they existed well before the first archeological evidence appeared, and furthermore, the lineages of early crops are still alive today:

that's how (in)valuable they are. Their study from the perspectives of ethnological botany and PGR conservation and use is as rich as it is far from ended. Given that food plants are most valuable to humankind we focus on the plants that are used and treasured by rural communities, the ones that are the source of their livelihoods: maize and the cultures it sustains, for one thing, but much more than that, the domesticated PGR of Mesoamerica that are many and important to agriculture and rural development.

A strict delimitation of Mesoamerica is unnecessary to our aim; in fact we adopted a much wider geographical perspective with the purpose of contrasting situations, revealing patterns, and contradictions. Thus, we included neighboring countries and peoples as well, with whom we share heritage, resources and cultures, as well as trade and industrial interests. This comparative approach includes the continental countries from Canada to Colombia and provides a wider context that is useful in framing issues at various levels: the multilateral frameworks, national or State Party obligations, and the rights thus recognized individually or collectively to rural communities, to farmers and indigenous peoples.

Background and basic information on human rights, heritage, biological resources, and industrial property rights is provided in which the legal doctrines and the law itself are the main source of context and principles. Table 22.1 presents the membership status by country to the various legal instruments here reviewed; it is a description of the primary global architecture of ESC as they relate to cultural and natural heritage, PGR, and industrial property.

The Universal Declaration on Human Rights [1], hereafter referred to as the Declaration, was unanimously adopted by the General Assembly of the United Nations in December 1948. As a Declaration it is an action of the general assembly that reflects aspirations but it is not hard law [10]. Nonetheless, it has generated mandate to formulate conventions, protocols, and covenants that derive from its principles, spirit, and text. This process was neither easy nor fast: it took three decades for the declaration to become international law. Two international covenants were submitted in 1953, one on civil and political rights and the other on ESC; it took until 1966 for approval of the text and they came into force until 1976. The Covenant on Civil and Political Rights addresses immediate and absolute rights such as human dignity and nondiscrimination; on the other hand, and as foundation for our main argument, the Covenant on Economic, Social and Cultural rights [2] expresses the rights that if fulfilled would in fact provide freedom from want and need. Each human right by itself cannot be fulfilled without the other; however, focus on the ESC is useful because they contain [2] the principles of human rights that should support the implementation of natural and cultural heritage, biological resources, and industrial property regulations.

World heritage in the United Nations Educational, Scientific and Cultural Organization (UNESCO) context has two main conventions, one on cultural and natural sites adopted in 1972 and one on cultural intangible domains, adopted 30 years later. The UNESCO Convention concerning the Protection of the World Cultural and Natural Heritage [3] now has a consolidated strategy worldwide as well as mirror initiatives at national, state, and even local levels. Although cultural

Table 22.1 Selected legal instruments relevant to economic, social, and cultural rights

	Human rights	Heritage		Resources		Industrial property		
	Economic, social, and cultural	Natural, cultural, intangible		Biodiversity and agriculture		Plant varieties and geographical indications		
Document	ICESC	WCNH	ICH	CBD	ITPGR	PARIS	UPOV	TRIPS
First signed	*1966*	*1972*	*2003*	*1992*	*2001*	*1883*	*1991*	*1994*
Canada	1976	1976	*nm*	1992	2002	1923	1991	1995
USA	1977	1973	*nm*	1993	2002	1887	1981	1995
México	1981	1984	2005	1992	*nm*	1903	1997	1995
Guatemala	2009	1979	2006	1995	2006	1998	*nm*	1995
Belize	2000	1990	2007	1993	*nm*	2000	*nm*	1995
El Salvador	1967	1991	2012	1994	2003	1993	*nm*	1995
Honduras	1966	1979	2006	1995	2004	1993	*nm*	1995
Nicaragua	1980	1979	2006	1992	2002	1996	2001	1995
Costa Rica	1966	1977	2007	1992	2006	1995	2009	1995
Panama	1976	1978	2004	1992	2006	1996	1999	1997
Colombia	1966	1983	2008	1994	2002	1996	1996	1995

Includes world cultural and natural heritage; biological and plant genetic resources; and industrial property instruments. Legal status for selected countries, including year of membership or not member (nm)

ICESC International Covenant on Economic, Social and Cultural Rights, *WNCH* Convention concerning the Protection of the World Cultural and Natural Heritage, *ICH* Convention for the Safeguarding of the Intangible Cultural Heritage, *CBD* Convention on Biological Diversity, *ITPGR* International Treaty on Plant Genetic Resources for Food and Agriculture, *PARIS* Paris Convention for the Protection of Industrial Property, *UPOV* International Convention for the Protection of New Plant Varieties, *TRIPS* Agreement on Trade-Related Aspects of Intellectual Property Rights

sites are mostly dedicated to architecture, some of them are landscapes, and although natural sites tend to include scenery more than resources, they do include important biological resources. Recently, cultural and natural criteria are being invoked in their mixed character as cultural landscapes and relevant areas and biological resources are being considered as part of this heritage.

The Convention for the Safeguarding of the Intangible Cultural Heritage [4] is more recent and awaiting consolidation, it addresses human creations that are not tangible, they are not sites but practices; and among other domains it recognizes languages as well as agriculture and food cultures, both substantial to the knowledge and use of PGR.

Before 1992, PGR were considered heritage of humankind. The CBD [5] signed at the Rio Summit not only includes conservation obligations to state parties, it specifically recognizes countries sovereignty over their biological and genetic resources—the biotic components with value, actual or potential to humanity—which directly derive from recognizing self-determination as a human right of peoples. A decade later came the International Treaty on Plant Genetic Resources for

Food and Agriculture [6] that includes a facilitated access scheme based on material transfer agreements (MTA) for resources that are deemed of a strategic nature. They also reflect the genetic resources that are deposited in the infrastructure of international agricultural research centers. In the area of genetic resources, the CBD generated the Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits arising from their Utilization.[1] The latter has been signed by the number of required parties and came into force in 2014, so it is an additional framework to consider in the short term but it is not addressed here. Finally, PGR are also being used as components of industrial property claims with differing degrees of creativity or inventiveness, as well as of public and private components. Since intellectual property is a wide-ranging issue, we only address PGR in the areas of plant breeders rights and of geographical indications. PGR are essential components in the vindication of plant breeder's rights since specific genotypes/phenotypes are registered. They are also essential components of the raw materials and qualities, the specific germplasm being used or the populations being managed is described as part of the protection of geographical indications (GI) used in trade to differentiate products derived from cultivated, managed, or wild biological resources. In both these types of industrial property, there are private aspects that imply exclusions but they also may, under certain conditions, contribute to creating public goods.

The globalization of industrial property started earlier than the internationalization of human rights, and the Paris Convention [7] of late nineteenth century is at the core of "modern" capitalism and its globalization through trade.

A *sui generis* system for the protection of new plant varieties was developed through a specific Union [8] whose mandate is to protect private rights to breeders over specific plant varieties that are homogeneous, novel in a certain sense and stable, they are the commercial component of the gene pool of a species, which in a wider sense is understood as PGR. Ornamentals and food crops are at the forefront of plant breeders rights (PBR) applications within the UPOV framework. In the late twentieth century, these frameworks have been integrated in a trade-related intellectual property rights agreement [9] in the framework at the World Trade Organization. In all the legal documents cited,[2] parties assume obligations to adequate national legal instruments and other policies and specific actions in order to protect human rights, recognize sovereignty over natural, biological and genetic resources, including respect and protection for traditional knowledge and practices, farmer's rights and intellectual property.

Not only governments or States must have obligations, but "all organs of society should endeavor to fulfill human rights." Therefore, we are all bounded, ethically and legally, to fulfill them, individually and collectively, acting as private or public entities. In addition, the regional comparative approach is pertinent because an

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[1] http://www.cbd.int/abs/

[2] This legal background represents the current state of affairs in terms of legal instruments available to countries in cultural or natural heritage, plant genetic resources and intellectual property in a context of domesticated and food plants. It is described as of late 2013 and the first semester of 2014.

international context that contributes to their fulfillment is also a human right as one of the conditions state parties should endeavor to achieve through cooperation ([1, art. 28], [2, art. 11]).

Before looking at the data, it is relevant to try to frame the issues and to state explicitly some definitions, basic principles, and assumptions of our analysis.

Resources and Heritage

Since our subject matter is PGR in relation to heritage, to their utilization and to industrial property, the meanings of resource itself provide clues on the core issues. Narotsky [11] indicates that a "resource is not one until it is known to be one by a human group," thus knowledge is key to resource "existence," and she further indicates certain conditions that are necessary to call something a resource:

> its presence must be known
> its useful aspects for human life must be understood
> the means to harness this aspect must be discovered
> the social organization must permit [its] exploitation [11, p. 9]

These straightforward conditions reveal the importance of knowledge, understanding, meanings, and social organization. If we think of domesticated plants and the knowledge and practices regarding their cultivation, transformation and use, the meaning of resource reveals that what is at stake are not only the seeds of agriculture but also the associated knowledge and practices: there are tangible and intangible components to this heritage. In addition, one should not forget that the tangible biological component is not a monument or a site, it is a living heritage constituted by the dynamic populations of cultivated species under management and selection by farmers and indigenous communities.

The governance and control of means, skills and knowledge that articulate access to PGR is part of what is changing: There is a "struggle over the access to and value of knowledge as a means of production" ([11, 25, pp. 21–25]) and this is evidence of a differential access to resources that expresses political and economic differences between groups of society. These power relations over resources are repeated or contested at different scales, it is knowledge and practices that are valuable and are being lost, appropriated, or used to resignify identities.

Heritage has a private or individual meaning that is a common understanding: we assume it is built through work; we inherit to our close descendants, our family, and extended family. If it is tangible, a material good, movable or not, it usually is private property in its strict sense and can be sold, rented, or otherwise disposed of. When shared by a community, a region, a people, it becomes heritage in its collective sense and it usually has inalienable components. Add the intangible dimension to this scaled depiction of heritage and the complexity becomes challenging for the law, for policy or social mobilization and action. Further adding to this equation, possible contradictory interests complicate coordinated action of the actors.

The proposal by Florescano is to contribute by trying to understand "the rationality that underlies the contradictions" because a critical historical perspective provides context to discuss heritage and resources [12].

García Canclini [13] suggests caution because it is processes that are of interest, not objects. Thus when fixing ideas of tradition or authenticity there are many risks, and this is particularly true for living resources and for cultural elements. Recall that agriculture and food harvesting, more than other human activities, require adaptation to environmental transformation. For humans, this social adaptation requires innovation and shared knowledge, because it implies "the use of old resources in new ways and the discovery of new resources in the old environment" [11, p. 14]. Practical skills attained through family, community, or simple practice are central to small-scale concepts of heritage, they are socially recognized knowledge incorporated into labor and this type of knowledge is substantial heritage in rural and peasant communities whose livelihoods depend on knowledge of the environment.

The perspective from history and heritage given by Florescano [12] integrates a critical interdisciplinary reflection from Mexico which is relevant because it is based on experience and developed in a cultural and legal matrix that is similar to other Latin American countries. Florescano [12] states that cultural heritage is being debated and among the issues that demand discussion is the redefinition of the idea of heritage, specifically by considering "the vindication of the intangible" or immaterial and reviewing and enrichment concepts, programs and regulations.

Before redefining cultural heritage, one must have a working definition. For Bonfil [14] cultural heritage is a set of assets:

> tangible or intangible, [that] constitute this heritage and wherein lies their importance, not only to the specialist or knowledgeable, but foremost to the common people [14, p. 28].

Thus, with a view from political anthropology he states that

> we all have culture, our own and particular culture [14, p. 30]

and beyond a simplistic reading of this statement of cultural relativism, the heritage of a people involves the

> cultural elements—some tangible, the others intangible—that a determined society considers its own and from which it takes hold to face its problems; to formulate and try to realize their aspirations and projects; to imagine, enjoy and express [14, p. 31].

With a contrasting emphasis but complementing one another, for García Canclini cultural heritage is

> what a social set deems as its own culture, that [which] sustains its identity and differentiates from other groups. Not only physical assets, but also the lived experience condensed in languages, knowledge, immaterial traditions, ways of using goods and physical spaces [13, p. 63].

Living heritage, cultural, natural and agricultural is affected by policies, economic trends, and globalization and this is why

> it is common to view as enemies the current processes of change: urban development, commoditization, cultural industries and tourism. [He proposes instead] to consider threats as

> context, […] not only because this are the conditions in which this assets exist, but because they contribute to rethinking what we should understand as heritage and as national identity [13, p. 57].

The understanding of contexts and of the determinants of what is considered heritage suggest clearly that what is now considered heritage is determined by dominant social groups and are thus selective, restrictive, and exclusive; they are linked to nationalistic projects while ethnic groups and their traditions are either marginalized or "folclorized" [12]. With Bonfil, there is agreement on being careful about nationalisms because they tend to obscure cultural, regional, or linguistic differences.

> There is no common heritage to all Mexicans" and this is "because there are diverse cultures within Mexican society and because there is social inequality in the possibilities of accessing cultural goods [14, p. 36]. Cultural differences only become contradictions and oppositions when the social systems in which they are based are linked between them by a relation of conflict [14, p. 51].

The recognition by various sectors of the importance of the intangible cultural aspects of heritage leads to the negotiation and eventual adoption of a convention on the intangible cultural heritage of humanity: it is the result of decades of discussion on new concepts and possibilities. Among its beneficial effects is the aim of preserving the integrity of the meaning of each activity selected [15], Arizpe indicates that it is a novel mechanism that will need to be built slowly "because the inherent idea of flow is implicit in intangible cultural heritage." She warns on the risks of trivialization of heritage; this threat is manifested when the most visible cultural actions are emptied or void of their sense through tourism and merchandising which critically are given a collectively appropriated meaning.

Biocultural diversity is a relatively new construction that provides focus on a wide recognition that certain forms of diversity in which life and culture are inextricably linked; and that it is in the intangible linguistic component that inextricability lies [16]. Linguistic heritage is so important because, in Possey's words, communities

> often possess a conservation ethic developed from living in particular ecosystems" and "without favorable conditions for the flourishing of language diversity, transmission of knowledge will break down—and with it the intricate management and livelihood systems that mold and maintain local biodiversity" [17, p. 394].

The local languages express in a unique form the elements of the environment and create specialized knowledge, agreements, or rules that use terms that reflect a specific socio-ecological process of adaptation. When an indigenous language disappears, a whole view of life is gone.

As an influential anthropologist, Possey had no doubt that traditional knowledge and practices could not be protected or recognized properly if not framed as a human rights issue [17] inherent to indigenous peoples self-determination. He was well aware of the risks of using the past and the present as only reference because tradition is a filter through which innovation occurs. Concurring with this view, is the declaration of the Four Directions Council of Canada that

> antiquity is not what defines traditional knowledge, but the way in which it is acquired and used [17, p. 381].

We are dealing with an informal innovation system and a formal one, which is both public and private; the aim of preserving and using PGR requires a respectful development of both systems, if viewed as a two-way road it should concern us that no one is run over on either side [10].

Mesoamerica, our region of interest, is an example of ecologically complex agricultural systems, it is a center of diversity of PGR that constitute the essential world crop genetic heritage. It also is a biologically diverse region with equivalent cultural diversity that includes the traditional knowledge of non-domesticated biological resources. Note that we do not use the word "wild," recalling the warning by Possey that "wilderness" as empty, unknown land and resources is a good example of "politically dominant scientific terminology" as prejudicing the "values" of territories.

It is perhaps why it is always important to consider that the vindications of indigenous peoples and farmers organizations are not expressed as a desire to own intellectual property, but to avoid piracy, privatization, or loss through trivialization. As indicated in Point 7 of the COICA[3] declaration on intellectual property rights and indigenous peoples:

> For members of indigenous peoples, knowledge and determination of use of resources are collective and intergenerational. No indigenous population, whether of individuals or communities, can sell or transfer ownership of resources which are property of the people and which each generation has an obligation to safeguard for the next [17, p. 389].

These concerns on their cultural and intangible heritage are expressed in the CBD as traditional and innovative knowledge and practices of local and indigenous communities (TK, in short, but without forgetting its full content). In a similar manner, these concerns found their way into the International Treaty on Plant Genetic Resources for Food and Agriculture as farmer's rights. Brush [18] arguments that conceptually and ethically the traditional knowledge and farmers rights can be merged in discussions. We share this view in principle as it is helpful to avoid considering them separately; but differences between them should be kept in mind. PGR are in themselves "a space of economic, political and symbolic dispute" and this space as in other forms of heritage involves the interests of three types of agents: the private sector, the State, and the social movements [13, p. 66]. All three actors may have ambivalent relations with heritage, stressing that black and white views are not useful: although private actors may even participate in destroying heritage, sometimes they recognize that its symbolic value increases the economic component of value; the State will value its integrating nature but also validate or participate in its destruction either by inaction or by supporting political or economic interests that do not have heritage concerns; social movements, if in dire need and urgency, may feel distant from the conservation of symbolic values, particularly if they are not theirs [13, p. 69].

The World Intellectual Property Organization established Fact Finding Missions on intellectual property and traditional knowledge, genetic resources and folklore [19] whose results provide a useful technical overview of the intellectual property

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[3] Coordinating body of indigenous organizations of the amazon basin.

issues involved in the protection of traditional knowledge. The technical, legal, and administrative challenges are considerable, basic concepts are as fundamental as they are contested: traditional, authentic, original, the notion of author or of public domain among others [20].

In slippery subjects such as intellectual property (IP) and heritage, it is important to state principles, givens, and ethics. For a biologist, owning life forms is in many senses absurd, but it is happening. The ethics of life and conservation are one primary source of conduct for a biologist, but they are not the only one, on the same standing ground and without prioritizing one over the other should be the ethics of human rights and pragmatic respect for them. Since our focus is on domesticated plants, the only way to achieve conservation in a dynamic and ethical manner is with the people that are agricultural and rural producers. Thus it is the viability of rural livelihoods that has to be (re)cognized as a goal and its (re)signification in a context of change should not focus on preserving tangible genetic material as an isolated activity because in the long term ecological and cultural processes are the most important resource [21]. Scientific and legal reductionist views dissect and fix an object in time and space. It is the everyday practices of farmer and indigenous people's communities that is the core of in situ conservation: their crops, their knowledge and practices are perhaps the most sophisticated result of the nature culture relation in the history of mankind.

The domesticated and wild plant resources of Mesoamerica and their conservation then require that the livelihoods of rural communities and the tangible and intangible cultural heritage they safeguard are fully recognized for its outstanding importance to humanity and real and effective measures are taken to support this communities. Cultural and natural heritage vindications and actions, the sustainable use of biodiversity's components, control over resources, public innovation in crop development, and collective forms of intellectual property may all play a role in reducing inequalities in the "free" market. That being said, one cannot be naïve in respect of issues of the privatization of public goods: this is happening in heritage, biological resources, and intellectual property contexts, and this is the reason why it is useful to consider them seriously in context of human rights and the self-determination of peoples and nations.

Human Rights Come First

In the Universal Declaration of Human Rights (UDHR), principles such as the "inherent dignity and of the equal and inalienable rights of all members of the human family" are stated, including the right to "enjoy freedom of speech and belief […] free and equal in dignity and rights, no discrimination, security and the protection of physical integrity, asylum, etc.…". It is a declaration of principles of law to protect individuals. Because a human right is a universal entitlement, its implementation should be measured by the degree to which it benefits those who have hitherto been the most disadvantaged and vulnerable [22].

The Declaration was a post World War II development that in a sense was a reaction to the evidence on how far nationalism could go concerning the use of "science" to justify genocide and contribute to the creation and use of weapons of mass destruction. However, the Declaration has deep roots in the end of colonialism and monarchies, in the bill of rights in early history of the USA: it expresses the minimum civil and political rights which need to be guaranteed in order to preserve the dignity and freedom of human beings. Human rights are a mechanism that was needed in order to limit this overwhelming bureaucratic powers of modern states. Their evolution has responded to the needs and demands of societies and three distinct stages or so-called generations of human rights are commonly distinguished. A first stage of human rights is the development, based on the declaration, of binding instruments on civil and political rights: their principle is freedom and should have total satisfaction, and the specific expression of these rights is the covenant on civil and political rights (art. 1, art. 15). Their fulfillment is an indispensable element of the modern democratic state.

Second and third generation human rights have moral, social, cultural, and economic components. They are collective in nature, their principle is equality and their satisfaction is progressive. For third generation of rights, the so-called solidarity or people's rights, fraternity is the principle and their satisfaction relies on international cooperation.

The question is then if addressing ESC rights is a direct contribution to creating the conditions needed to fulfill the civil and the political ones. Thus, without forgetting civil and political rights, we will concentrate on ESC components of human rights from here on.

The common components from the Declaration and the Covenant on ESC rights are indicated in Table 22.2 and the fact that the covenant has treaty status highlights its importance. When reading these rights it is useful to keep in mind that PGR are our focus as well as the livelihoods that sustain the agricultural landscapes where these resources are alive, diverse and adapting; as well as they are threatened by various forces that shape agricultural practices and rural landscapes. At the same time, while revisiting these human rights, bear in mind individuals of all ages and gender with human rights, citizens and families, the rural communities, regions or peoples. When doing so, ESC acquire a special meaning and the challenges towards their fulfillment are different from those found in similarly unequal but urban societies.

The International Covenant of ESC recognizes to:

> All peoples […] the right of self-determination to freely dispose of their natural wealth and resources [2].

This principle is highly relevant because it expresses at a multilateral level between nations the sovereignty over biological resources in the CBD; it is however, a national attribution to implement this principles in relation to each nations rural communities.

A reaffirmation of basic rights from the Declaration but rephrased as an obligation of parties is expressed in article 2 which points out that insofar as possible countries should:

Table 22.2 Common components of the universal declaration of human rights and the economic, social, and cultural rights covenant

Everyone has the right to: [Recognize the right of everyone to:]	DHR	ESC
own property alone as well as in association with others	17	
freedom of peaceful assembly and association	20	
take part in the government of his country, directly or through freely chosen representatives	21.1	
equal access to public service in his country	21.2	
social security and is entitled to realization of the economic, social, and cultural rights indispensable for his dignity and the free development of his personality	22	
the opportunity to gain his living by work which he freely chooses or accepts		*6*
the enjoyment of just and favorable conditions of work		*7*
[…] form trade unions and join the trade union of his choice, subject only to the rules of the organization concerned, for the promotion and protection of his economic and social interests	23.4	*8*
a standard of living adequate for the health and well-being of himself and of his family, including food, clothing, housing and medical care and necessary social services	25.1	
an adequate standard of living for himself and his family, including adequate food, […] and to the continuous improvement of living conditions		*11.1*
the fundamental right of everyone to be free from hunger		*11.2*
Parties		
(a) improve methods of production, conservation and distribution of food by making full use of technical and scientific knowledge, by disseminating knowledge of the principles of nutrition and by developing or reforming agrarian systems in such a way as to achieve the most efficient development and utilization of natural resources		*11.2.a*
(b) taking into account the problems of both food-importing and food-exporting countries, to ensure an equitable distribution of world food supplies in relation to need		*11.2.b.*
participate [freely] in the cultural life of the community, to enjoy the arts and to share in scientific advancement and its benefits	27.1	
take part in cultural life		*15.a*
enjoy the benefits of scientific progress and its applications		*15.b*
benefit from the protection of the moral and material interests resulting from any scientific, literary or artistic production of which he is the author	27.2	*15.c*
a social and international order in which the [human] rights and freedoms can be fully realized	28	*11*

Numbers indicate articles from the Universal Declaration on Human Rights (UDHR) or the International Covenant on Economic, Social and Cultural Rights (ICESC). Brackets indicate text from the ICESC

> take steps […] to achieving progressively the full realization of the ESC […] including particularly the adoption of legislative measures [and to] guarantee that the ESC will be exercised without discrimination of any kind; [and to] ensure the equal right of men and women to the enjoyment of all ESC rights [2, art. 2, part 1–3].

In this sense, the state parties are the ones that have the obligations to act, as do public servants. The rights are recognized to people, to individuals, citizens and to their different collectivities.

The difference between the Declaration and the Covenant relies in the way that the Rights are recognized, in the Declaration "Everyone has the right to" while in the covenant states acquire the obligation to "Recognize the right of everyone to." This means that it is not enough to have rights but that States should guarantee their fulfillment.

Rules or agreements that determine ownership and governance at the local level are also affected by current change in rules and agreements at national and international level. Both formal and informal governance of activities are needed to recognize communities that hold PGR of worldwide importance and support their agricultural livelihoods. These livelihoods cannot be idealized in their current tragic reality: hungry, unequal and insecure, but as fulfilling all basic human rights as a precondition, wherever its costs. In the context of the articles that are highlighted in Table 22.2, it is interesting to note that:

> The family is the natural and fundamental group unit of society and is entitled to protection by society and the State [16].

The context of rural livelihoods requires that we understand that individuals, families, communities, and peoples have developed cultural resistance strategies that depend on agriculture, rangeland, and forest management.

"The preservation of cultural assets can never be more important than the people who need it to make a living" [13, p. 78], in other words, these means respecting human rights comes first and their fulfillment may benefit from respecting the use and conservation of natural and cultural heritage and resources, using collective rights as a central tool, be they self-determination and control over resources and knowledge, with or without intellectual property, formal heritage or other *sui generis* instruments.

Article 15 of the Covenant recognizes the issue of the right of the citizen to protect moral and material interest from which he is author. A human rights approach to intellectual property requires integrating principle with concepts, one finds that heritage, resource management and intellectual property, all gain from a perspective of human rights because it explicitly includes people, their well-being, and governance.

In order to achieve these objectives, the covenant goes into details of special importance to PGR because there is the obligation of parties to improve methods of production, conservation, and distribution of food [2 art. 11.2.a]. This is a priority that expresses the relevance given by parties to rural development and agriculture as means to achieve the goals of ESC. At the international level, these goals should consider and take into account the problems of both food-importing and food-exporting countries [2, art. 11.2.b].

These considerations of context are still relevant in the twenty-first century since the weight of food imports on total energy needs in Central America and Mexico has reached levels unimaginable four decades ago. This has to create conscience that nowadays the human right to food is dependent on solidarity between States. The United Nations Declaration on the Rights of Indigenous Peoples details rights related to cultural heritage, traditional knowledge and traditional cultural expressions and to intellectual property. It is a long article that expresses very well the extent of indigenous people's vindication on intangible elements of culture:

> Indigenous peoples have the right to maintain, control, protect and develop their cultural heritage, traditional knowledge and traditional cultural expressions, as well as the manifestations of their sciences, technologies and cultures, including human and genetic resources, seeds, medicines, knowledge of the properties of fauna and flora, oral traditions, literatures, designs, sports and traditional games and visual and performing arts. They also have the right to maintain, control, protect and develop their intellectual property over such cultural heritage, traditional knowledge, and traditional cultural expressions [23, art. 31].

Remember that this is a declaration and it will probably take decades to implement both nationally and in its multilateral components. This is also important while analyzing legal obligations that are national and in which soft and hard obligations can be differentiated and will be highlighted now and then. This does not necessarily mean that soft law is not important; it usually means that for sovereignty reasons in issues related to resources and heritage countries will not accept any extraterritorial attributions to other parties. However and by contrast, on issues of trade and others the "globalization" of rules is ruling.

In the following sections we provide a quantitative regional panorama of the extent to which biological resources are being registered as part of world cultural and natural heritage, as PGR for food and agriculture, as plant breeders rights, or as geographical indications. Current trends and developments are identified for the region and their potential effects on the study and conservation of PGR are highlighted when applicable.

World Cultural and Natural Heritage in Mesoamerica

The definitions of what shall be considered as heritage, the specific sites that shall be considered by the Convention concerning the Protection of the World Cultural and Natural Heritage are given in Table 22.3 and they clearly suggest its scope: sites of *outstanding universal value*. The common understanding of cultural heritage is mostly archeological, historic architecture, monumental; and even the natural heritage tends to be spectacular and beautiful, a landscape. However, the points of view invoked are not mutually exclusive, they share elements and they are sometimes recognized in mixed character. Recently, UNESCO defined a new category, the cultural landscape, that represents the "combined works of nature and humankind, they express a long and intimate relationship between peoples and their natural environment." Parties to the Convention should protect the tangible cultural and/or natural heritage "in so far as possible, and as appropriate for each country" and the primary duty of State is to create conditions for "ensuring the identification, protection, conservation, presentation and transmission to future generations of the cultural and natural heritage situated on its territory" [4].

Table 22.3 Conceptual components of cultural, natural and intangible world heritage law

World cultural and natural heritage		WCNH
[Given their] outstanding universal value	*from the point(s) of view of […]*	
the following shall be considered as "heritage"		
Cultural heritage		*1*
monuments: architectural works, works of monumental sculpture and painting, elements or structures of an archeological nature, inscriptions, cave dwellings and combinations of features	*history, art, or science*	
groups of buildings: separate or connected buildings which, because of their architecture, their homogeneity or their place in the landscape	*history, art, or science*	
sites: works of man or the combined works of nature and man, and areas including archeological sites	*historical, aesthetic, ethnological, or anthropological*	
Natural heritage		*2*
natural features consisting of physical and biological formations or groups of such formations;	*aesthetic or scientific*	
geological and physiographical formations and precisely delineated areas which constitute the habitat of threatened species of animals and plants;	*science or conservation*	
natural sites or precisely delineated natural areas.	*science, conservation, or natural beauty*	
Intangible cultural heritage	*Domains*	*ICH*
the practices, representations, expressions, knowledge, skills—as well as the instruments, objects, artefacts, and cultural spaces associated therewith—that communities, groups and, in some cases, individuals recognize as part of their cultural heritage.	*(a) oral traditions and expressions, including language as a vehicle […]; (b) performing arts; (c) social practices, rituals, and festive events; (d) knowledge and practices concerning nature and the universe; (e) traditional craftsmanship*	2.1 2.2

Articles, definition and points of view considered in the Convention concerning the Protection of the World Cultural and Natural Heritage (WNCH) and Convention for the Safeguarding of the Intangible Cultural Heritage (ICH)

The commitments by parties to the Convention Concerning the Protection of the World Cultural and Natural Heritage (CNH) are to implement:

> Effective and active measures; a general policy which aims to give the CNH a function in the life of the community; comprehensive planning programs; services, scientific and technical studies and research; operating methods capable of counteracting the dangers; appropriate legal, scientific, technical, administrative and financial measures; national or regional centres for training; and to encourage scientific research [3, art. 5].

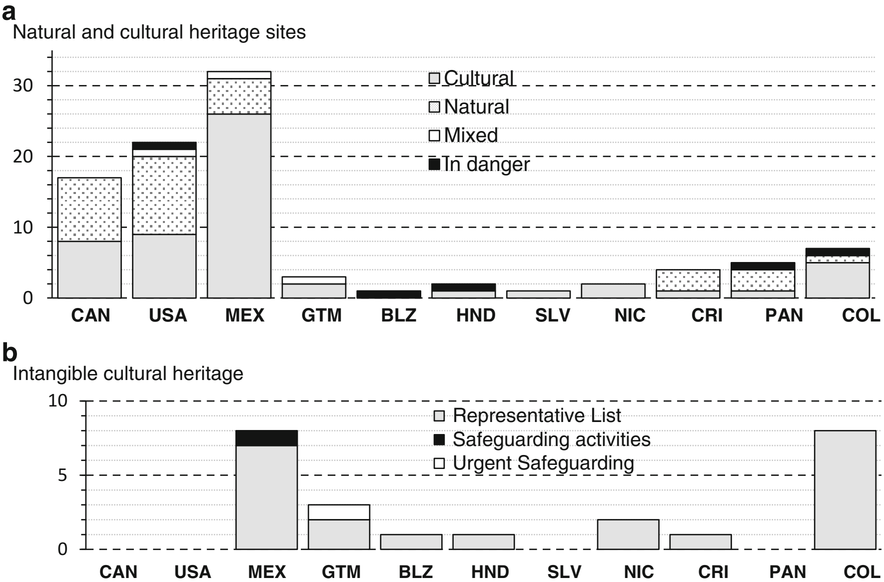

Fig. 22.1 Number of registered world heritage by country and category in selected countries. (**a**) Two WCNH sites are shared by USA and Canada and one by Panama and Costa Rica. (**b**) One ICH declaration is shared by Belize, Guatemala, Honduras, and Nicaragua. List of ICH in Need of Urgent Safeguarding is composed of elements that require urgent measures. The Register of Best Safeguarding Practices contains programs, projects, and activities that reflect the principles and the objectives of the Convention. The Representative List is made up of elements that demonstrate the diversity of this heritage and raise awareness about its importance

These activities should consider all the tangible components described in Table 22.3 as well as the points of view that are further developed as criteria.

It is interesting to note that this Convention has no specific exceptions to its implications, the language is careful, progressive and obligations are, in a sense, soft law. These forms of protection of heritage existed well before sovereignty over genetic resources was even spoken of. However, heritage was and still is a relevant legal, political, social and cultural construction and reference, so the status of these world heritage protection efforts deserves a panoramic view of the heritage that parties are deeming as representative, as well as the innovations that are taking place.

In Fig. 22.1a, the current numerical status of world heritage registered sites for Mesoamerican countries and their neighbors is shown according to UNESCO's website,[4] which is in itself a good expression of the level of consolidation that this strategy has worldwide. Overall, the region has 96 national designations corresponding to 93 sites, three of them are shared by two or more countries. By category, we find 56 cultural sites, 24 natural sites, 5 in danger and 3 of them are mixed.

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[4] www.unesco.org

Canada, USA, and Mexico account for more than 70 % of all the heritage sites in the region and almost the 80 % of the natural sites.

Canada has obtained 17 declarations and the USA 22 with a dominance of natural sites. Considering that two natural sites are shared these two countries have a total 37 UNESCO sites, which represent almost 40 % of the total of WCNH sites in the region and more than 60 % of the natural sites. Their most frequent criteria are beauty, aesthetic importance and earth's history, geology, and represent the criteria used with the highest frequency. The new cultural landscape category has been used by Canada with the Grand Pré marshland.

There is a shared site[5] with an incredible area of 9,839,121 ha. The remaining natural sites of Canada have an average of area close to one million of ha and in the USA is close to 300,000 ha. The USA has a site that is in danger; the Everglades National Park in Florida and the main risks to this site are the water flow reduction and nutrient pollution. In the other hand, the unique mixed cultural and natural site Papahānaumokuākea in the Pacific ocean has 36,207,499 ha, which is described as an area with "deep cosmological and traditional significance for living Native Hawaiian culture, as an ancestral environment, as an embodiment of the Hawaiian concept of kinship between people and the natural world."

Some national parks of the USA are also world heritage sites. Of interest to our discussion is the value of the biological resources contained in these areas. The hydrothermal vents of Yellowstone contained the microbial diversity that lead to the discovered by Thomas D. Brock in 1968 of *Thermus aquaticus* from which the Taq polymerase was isolated and further developed as a central component of a multimillion dollar industry for pharmaceutical and biotech companies [24]. We know by fact then that "unknown" resources can be really valuable and that there was no retribution to the park whatsoever. It could be argued that the US biotech industry and US citizens benefited from this process as whole. However, in the late nineties of the twentieth century, the Park reached a deal with the Diversa Corporation to prospect in the area and provide benefits to the park. However, a judge suspended the agreement because the National Park Service and the Department of the Interior did a deal without the knowledge and consent of the owners of the parks: the people of the USA.[6] The relevance of this case lies in the fact that a common law country, that leads the world in life patenting strategies, sets precedent on the extent to which governments may dispose physically or otherwise of national natural heritage.

México has 32 sites, more than a third of the regions total, more than 80 % are cultural. The most frequent criteria used are architecture, technology landscape and architecture, monumental. The five registered natural sites have an average of area of more than 450,000 ha. A special mention to the Agave Landscape and Ancient Industrial Facilities of Tequila (35,019 ha) is warranted since it represents cultural

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[5] This site includes the Kluane, Wrangell-St. Elias, Glacier Bay and Tatshenshini-Alsek specific areas.

[6] Wild Rockies Networker. The Quarterly Journal of Alliance for the Wild Rockies. Vol. 1. No. 1. Winter of 1998 in http://www.wildrockiesalliance.org

landscapes and magueys are an iconic domesticated crop of Mesoamerica while the geographical indication Tequila is one of the world's most valuable. The roots of the modern day tequila industry are old but the natural, cultural, and social link to that history and microregions is now weak: there has been an expansion of plantations way beyond its original environment, a reduction of genetic diversity in the blue agave variety, as well as intensive technical change and foreign investment. The journal that promotes and debates cultural heritage and tourism is edited by the national arts and cultural council[7]; and this reflects the economic interest and the policies to promote the tourism related to cultural heritage in developing countries.

Mexico now has its first mixed site, the Ancient Maya City and Protected Tropical Forests of Calakmul, Campeche in the south of Mexico that was recently declared.

Centroamerica has eight cultural sites, five natural, one mixed, and three in danger: altogether a fifth of the total of sites in the studied region. Guatemala has three sites, one of which is the Tikal National Park that has a mixed character and is located in the same ecological and cultural area as Calakmul in Mexico. This regional dimension of heritage is also expressed by the Belize Barrier Reef Reserve System, the largest barrier reef in the Northern hemisphere, this site, unique designation in Belize, is registered as In Danger. UNESCO refers to mangrove cutting and excessive developments in the property as the main problems. This site is part of the Mesoamerican Barrier Reef System which is located in the Caribbean Sea, along territory of Mexico, Guatemala, Belize and Honduras. El Salvador and Honduras have a cultural site each. Nicaragua has two cultural sites. Costa Rica has four sites, three are natural with an average near to 300,000 ha. Honduras has a site categorized In Danger: the Río Plátano Biosphere Reserve was selected with the aim of mobilizing support for its preservation. Panama leads in Central America with five sites, one cultural, three natural—with an average area of near to 500,000 ha, and one In Danger. Costa Rica and Panama have a shared natural site which includes the Talamanca Range, La Amistad Reserve, and La Amistad National Park.

Colombia has seven sites (five cultural, one natural, and one In Danger). The four cultural criteria most frequently used are tradition, civilization, architecture, technology landscape, human environment interaction and living traditions, ideas, and beliefs. The Los Katios National Park is the only site registered as in danger since it is threatened by deforestation due to the illegal extraction of timber, also suffering illegal fishing and hunting. Mixed cultural and natural criteria are invoked for the legacy of coffee culture.

The average number of criteria invoked is detailed in Table 22.4: overall, 2.4 is the average number of criteria used. Values below this average suggest the specificity of sites while higher values suggest an integrated approach. Since not only one criteria is used, the total of sites by country is less than the number of criteria used, which are given in the last row of the table.

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[7] Consejo Nacional para la cultura y las artes. Patrimonio cultural y turismo. Cuadernos, Consejo Nacional para la Cultura y las Artes (CONACULTA).

Table 22.4 Criteria used for designation of cultural and natural heritage sites in selected countries

Country	CAN	USA	MEX	GTM	BLZ	HND	SLV	NIC	CRI	PAN	COL	Total
Selection criteria												
Average number of criteria per site	1.9	2.3	2.7	3.7	3.0	3.0	2.0	2.0	2.3	2.8	1.7	2.4
Total sites	17	22	32	3	1	2	1	2	4	5	7	*96*
Frequency of criteria												
Cultural												*0.58*
1. *Masterpiece, genius*	0.03	0.04	0.13	0.18	–	–	–	–	–	0.07	–	*0.07*
2. *Architecture, monumental*	–	–	0.26	.18	–	–	–	.25	–	0.07	–	*0.11*
3. *Tradition, civilization*	0.06	0.10	0.16	0.18	–	–	0.50	0.25	0.11	–	0.17	*0.12*
4. *Architecture, technology landscape*	0.13	0.06	0.24	0.27	–	0.17	0.50	.50	–	0.14	0.17	*0.17*
5. *Human environment interaction*	0.06	–	0.02	–	–	–	–	–	–	–	0.17	*0.03*
6. *Living traditions, ideas, beliefs*	0.13	0.10	.05	–	–	0.17	–	–	–	0.07	0.17	*0.07*
Natural												*0.42*
7. *Beauty, aesthetic importance*	0.22	0.20	0.05	–	0.33	0.17	–	–	0.11	0.14	0.08	*0.12*
8. *Earth's history, geology*	0.22	0.20	0.01	–	–	0.17	–	–	0.11	0.07	–	*0.09*
9. *Ecological and biological processes*	0.09	0.18	0.02	0.09	0.33	0.17	–	–	0.33	0.21	0.17	*0.11*
10. *Natural habitats, in situ conservation*	0.06	0.14	0.06	0.09	0.33	0.17	–	–	0.33	0.21	0.08	*0.10*

A total of 93 different sites are registered in the region. Frequency was estimated with a $n=96$ to account for the redundancy of shared sites: two shared between Canada and the USA, and one between Panama and Costa Rica

Canada and USA use the beauty, aesthetic importance, earth's history, geology, and ecological processes as their most frequent criteria, accounting for one out of every five criteria invoked. Mexico has a different focus and is the only one country that has used all ten points of view: architecture, monumentality and technological landscapes are the most frequent, accounting for one out of every four criteria invoked. There is an obvious trend towards prehispanic monumentality and colonial groups of buildings. This is true for the rest of region since the highest total frequency (0.17) is the architectural and technological landscapes.

Guatemala considered cultural criteria in all its sites, and the natural ones had the lowest frequency, it is only used in a mixed site. On the other hand, Belize, Honduras, El Salvador, and Nicaragua have only one or two sites. Costa Rica and Panama have natural criteria as the most frequent and it represents one third and one fifth of the criteria they have used. Colombia uses cultural criteria twice as much as natural ones. Finally, overall the region shows a balance between the use of cultural and natural criteria, while the least invoked criteria are human environment interactions, living traditions and beliefs, as well as masterpieces of human genius.

The outstanding universal value of these sites is the main reason they reach the list; however, all the countries analyzed have protected areas systems which are national in situ conservation strategies. In the cultural and natural heritage areas, states and local level authorities are also registering sites, so, the examples here described are representative of what countries consider of outstanding value as representative. International cooperation is key in consolidating these strategies. Although the link between world heritage registration and biological and genetic resources management may seem weak, we found a clear relation to traditional communities and indigenous peoples original territories, as well as relevant agricultural landscapes that have millenary continuity and are now living heritages.

Intangible Cultural Heritage

The link between tangible cultural and natural heritage and the intangible component developed into a convention three decades after the sites approach. It is not perhaps consolidated but implementation is ongoing and shows interesting links to biological and genetic resources, as well as to linguistic diversity.

The convention on intangible cultural heritage has safeguarding as its main purpose. By safeguarding the convention means:

> measures aimed at ensuring the viability of the intangible cultural heritage, including […] identification, documentation, research, preservation, protection, promotion, enhancement, transmission, particularly through formal and non formal education, as well as the revitalization of the various aspects of such heritage [4 art. 2.2].

Note that intangible heritage is not defined as such, but what is considered is enumerated in Table 22.3. A description of the attributes of intangible cultural heritage includes that it is:

> transmitted from generation to generation; [it is] constantly recreated by communities and groups in response to their environment, their interaction with nature and their history, and provides them with a sense of identity and continuity, thus promoting respect for cultural diversity and human creativity [4 art. 2.1].

Then, when the subject matter and the domains have been described, given meaning and attributes, it is easier to understand the challenges and importance of the purposes of this Convention, which are:

> to safeguard the intangible cultural heritage; to ensure respect for the intangible cultural heritage of the communities, groups and individuals concerned; to raise awareness at the local, national and international levels of the importance of the intangible cultural heritage, and of ensuring mutual appreciation thereof; [and] to provide for international cooperation and assistance [4 art. 1a–d].

Within the convention there are three categories: being representative of diversity worldwide; those that require urgent measures; and a register of best practices in protecting endangered heritage. Rephrasing the Conventions obligations, in the website the meaning of each category is explained:

> Representative List of the Intangible Cultural Heritage of Humanity: State parties propose to the Committee of the Convention those intangible heritage elements that demonstrate the diversity of this heritage and raise awareness about its importance.
>
> The List of Intangible Cultural Heritage in Need of Urgent Safeguarding: composed of intangible heritage elements that concerned communities and States Parties consider require urgent measures to keep them alive.
>
> The Register of Best Safeguarding Practices contains programs, projects and activities that best reflect the principles and the objectives of the Convention.

Thus, representativeness is of the utmost importance, urgency leads priorities and being inscribed as endangered should aid in mobilizing cooperation within the convention and to implement assistance for those that undertake the measures to safeguard these heritage.

In Fig. 22.1b, the currently registered intangible cultural heritage is shown. There are currently more than twenty designations for the region; one is shared by four countries, thus, there are in total 24 national designations. Canada and the USA are not members to the Convention, perhaps because of their concerns of conflict with intellectual property. Mexico and Colombia are leading the area in registered intangible cultural manifestations with 16 of the 20 designations.

Of particular importance to the issue of PGR for food and agriculture, is the case of the Traditional Mexican cuisine file, which is further, detailed as an ancestral and ongoing community culture. The first attempt by Mexico in 2005 to register its cuisine emphasized maize culture[8] and UNESCO argued that the symbolic and ritual elements were not adequately described, thus rejecting the inscription. Five years later, based on the specific innovative work with communities in Michoacan

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[8] Consejo Nacional para la cultura y las artes. Patrimonio cultural y turismo. Cuadernos 10. Pueblo del maíz. La cocina ancestral de México. México, D.F.: El expediente ante la UNESCO, Consejo Nacional para la Cultura y las Artes (CONACULTA); 2005.

the proposal was accepted.[9] In UNESCO's description, the Traditional Mexican cuisine:

> Is a comprehensive cultural model comprising farming, ritual practices, age-old skills, culinary techniques and ancestral community customs and manners. It is made possible by collective participation in the entire traditional food chain: from planting and harvesting to cooking and eating.

The Michoacan paradigm involves collectives of female cooks and other practitioners whose:

> "knowledge and techniques express community identity, reinforce social bonds, and build stronger local, regional and national identities…" and it is described "as a mean of sustainable development".

The extent to which the development of this registered cultural heritage will also support local agriculture and the use of specific PGR as components of traditional and local gastronomies remains to be seen. A national level inventory of recipes, processes, and ingredients is an ongoing task being developed in several stages and there is a civil association in which the State and other stakeholders are represented and it is called the conservatory of Mexican gastronomic culture.[10]

Complementary to knowledge and techniques, languages themselves are a reservoir of knowledge about nature, biological and genetic resources. The *Paach* Ceremony in Guatemala involves an interesting signification of natural and cultural heritage linked to language. Among its three designations, Guatemala registered this ceremony as in Need of Urgent Safeguarding. It is described by UNESCO as a heritage that:

> Strengthens the identity of the community of San Pedro and its knowledge and respect for nature and its conservation.

This ceremony has a deep agricultural origin and its intention is to thank for the harvest and prayers are in the Mam language; the individuals that lead the ceremony and prayer are known as *parlamenteros*. This type of heritage that links cultural expressions with the natural world is facing many threats around the world.

A dramatic example is that of the Garifuna, in their language, dance and music is heritage registered by four countries: Belize, Guatemala, Honduras, and Nicaragua. This expression is a mix of African and Amerindian elements based on their history and traditional knowledge, it considers explicitly their livelihoods: cassava-growing, fishing, canoe-building, and the construction of baked mud houses. Nowadays it is taught in only one village by elders, and face discrimination, migration and exclusion from the formal system of education are serious risks for its maintenance.

In Colombia there is the Traditional knowledge of the jaguar shamans of Yuruparí and the *Wayuu* normative system, applied by the *Pütchipü'üi* or *palabrero*,

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[9] Interview to Gloria López Morales by Alberto Nájar in BBC Mundo, September 25, 2009. Cocina mexicana, El patrimonio cultural?. In www.bbc.co.uk

[10] www.ccgm.mx

this nomination "could promote respect for cultural diversity and encourage dialogue concerning indigenous traditional knowledge and practices."

Perhaps the complementarity between heritage sites and intangible heritage is not so obvious and perhaps collateral to PGR. The challenges and opportunities faced by world cultural and natural heritage are at least a useful source of experience for the communities and stakeholders interested in agriculture; and in the best case, a pragmatic strategy to protect and value these living heritages.

Natural, Biological, and PGR

Legal definitions of biodiversity, biological and genetic resources are a novelty. The precedent is natural resources, of which the biotic elements are but a component. Definitions of natural resources in national laws are described briefly to show that there are differences and they are not subtle. Some tend to be descriptive, not conceptual, and they enlist everything that is considered, land, soils, and water. In Canada for example, for the Department of Natural Resources Act a natural resource means:

> mines, minerals and other non-renewable resources, energy, including energy developed from water, and forest resources [25 art. 2].

Biodiversity and biological resources are clearly excluded from this act, since they are covered elsewhere in Canadian law under the specific Act covering species at risk and wildlife. In the case of Mexico, there is an abstract definition, a natural resource is the:

> natural element susceptible of being used [or exploited] in the benefit of mankind [26 art. 3, xxiv].

The definitions of Biodiversity and biological resources in Mexico are codified in the environmental protection Act and are textual from the CBD. The case in Costa Rica is that the biotic component is explicit.

> Natural resource: all element of biotic or abiotic nature that is exploited, be it commercial or not [27, art. 28].

In the case of Colombia the definition is extensive, and in the natural resources concept they detail that it includes watersheds, rivers, including superficial and subterranean waters, forests, species of fauna, national marine waters and the elements they contain, the atmosphere and geothermal deposits [28, art. 11].

The Convention of Biological Diversity (CBD) is built on the all encompassing concept of biodiversity that includes the diversity of life: of ecosystems, of species and genes. The objectives of the convention [5 art. 1] are the conservation of biodiversity, the sustainable use of its components, and the equitable sharing of the benefits arising from access to genetic resources. This is a careful construction, the words biological and resource are not in the definition of objectives as such, but the sustainable use of the components of biodiversity is included, sovereignty is reflected in the fact that in situ conservation and sustainability in biological resources use are national obligations and attributions, while the issue of equitable sharing of benefits relates specifically to access to genetic resources is in the multilateral domain, there are obligations between parties.

It is useful to look at the definition of biological resources contained in the CBD, it includes

> genetic resources, organisms or parts thereof, populations, or any other biotic component of ecosystems with actual or potential use or value for humanity.

Genetic resources means

> genetic material of actual or potential value

and genetic material means

> any material of plant, animal, microbial or other origin containing functional units of heredity.

These concatenated definitions show the degree of dissection that is being implemented under the sovereignty logic of the CBD. Reductionism that goes into the specificity of genetic materials as policy or law allows for the development of markets and industrial property vindications, without further consideration of long-term consequences in terms of diversity, resources, and options for the future. It is useful to note that PGR for food and agriculture, genetic resources, and genetic material are all contained in the definition of biological resources. Plant varieties, are specific genetic materials commercially protected that are in themselves part of the PGR of a specific gene pool. In geographical indications (GI), biological resources are part of the characterization of the protected product or service.

A decade after the CBD was signed, a treaty on PGR for food and agriculture (PGRFA) was finally agreed. Table 22.5 summarizes their main components by comparing objectives, definitions, principle, scope, and substantive issues.

The objective of the treaty is limited to the conservation and sustainable use of PGR for food and agriculture and the equitable sharing of benefits is not tied to access to genetic resources but to their use. This reflects the fact that the PGR at stake within the multilateral system are already deposited ex situ in collections that are in trust in the multilateral system to which the treaty gave formality [29].

Among the terms defined in both conventions, we find ex situ and in situ conservation and genetic material. Terms that are similar suggest the delimited scope of the treaty: centers of origin and crop diversity as different from countries of origin or providing genetic resources. Nine terms are exclusive to the CBD and they clearly reflect its wide conservation and sustainability focus, while the exclusive terms of the treaty, variety and ex situ collection, clearly reflect the specificity of the PGR of interest.

The principle of the CBD is sovereignty of each party to exploit its own resources and the treaty specifies harmony with the CBD but does not explain exactly how this harmony can be reached. The substantive issues of both instruments clearly reveal their scope of interest: we highlight some of the differences while referring

Table 22.5 Selected components of the biodiversity convention and the treaty on plant genetic resources for food and agriculture

Convention on biological diversity		Plant genetic resources for food and agriculture	
Objectives			
Conservation of biodiversity, sustainable use of its components and access to genetic resources and benefit sharing	1	Conservation and sustainable use of PGRFA and the fair and equitable sharing of the benefits arising from their use	1
Terms defined	2		2
Shared			
Ex situ conservation, Genetic material, In situ conservation		Ex situ conservation, Genetic material, In situ conservation	
Similar			
Biological resources; Genetic resources		Plant Genetic Resources for Food and Agriculture	
Country of origin of genetic resources, Country providing genetic resources		Center of origin, Center of crop diversity	
Exclusive			
Biological diversity, Biotechnology, Domesticated or cultivated species, Ecosystem, Sustainable use, Habitat, In situ conditions, Protected area, Technology		Variety, Ex situ collection	
Principle			
Sovereign right to exploit their own resources	3	in harmony with the CBD	1
Jurisdictional scope			
Components of biological diversity within its national jurisdiction	4	Plant Genetic Resources for Food and Agriculture	3
Substantive issues			
Cooperation	5	National Commitments and International Cooperation	7
General Measures for Conservation and Sustainable Use	6	General obligations	4
Identification and Monitoring (*Annex I*). Ecosystems, Species, and Genes	7	Coverage of the Multilateral System: the PGRFA listed in Annex I by Crop and Genus	11
In situ Conservation	8	Conservation, Exploration, Collection, Characterization, Evaluation, and Documentation of PGRFA	5
Traditional and innovative practices of local and indigenous communities	8 j	Farmers' Rights	9
Ex situ Conservation	9	Ex Situ Collections of PGRFA held by the Agricultural Research Centers of the CGIAR and other International Institutions	15

(continued)

Table 22.5 (continued)

Convention on biological diversity		Plant genetic resources for food and agriculture	
Sustainable Use of Components of Biological Diversity	10	Sustainable Use of Plant Genetic Resources	6
Access to Genetic Resources	15	Multilateral System of Access and Benefit-sharing	10
Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits arising from their Utilization		Facilitated access to PGRFA within the Multilateral System	12
		Benefit-sharing in the Multilateral System	13
		Global Plan of Action	14
		International Plant Genetic Resources Networks	16
		The Global Information System on Plant Genetic Resources for Food and Agriculture	17

Number indicates articles

to [30] for an in-depth legal analysis of the implications of traditional knowledge and genetic resources regulation.

The CBD has one Annex on identification and monitoring of the components of biodiversity that describes components which should be prioritized due to their importance to life on earth or to humankind[11]; while the treaty has a similar annex with specific crops that are listed by genus and the scope is limited to them. In the intangible component, the CBD recognizes the traditional and innovative practices of indigenous and local communities while the treaty recognizes farmer's rights. Both these issues are intangible elements: they are culture and practices that were addressed in the heritage section and are here again seeing in a sovereignty framework; they will be addressed later on while describing current applications of plant breeder's rights in Mexico.

In the ex situ component, the CBD has mostly legal obligations and now has a Protocol specific to the issue of benefit sharing and access to genetic resources. This is perhaps the most important difference between these two instruments: the CBD is building a multilateral legal framework, the Nagoya Protocol, while the Treaty on PGR has supporting components that involve infrastructure and collections which

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[11] Annex I to CBD includes (1) Ecosystems and habitats: containing high diversity, large numbers of endemic or threatened species, or wilderness; required by migratory species; of social, economic, cultural or scientific importance; or, which are representative, unique or associated with key evolutionary or other biological processes; (2) Species and communities which are: threatened; wild relatives of domesticated or cultivated species; of medicinal, agricultural or other economic value; or social, scientific, or cultural importance; or importance for research into the conservation and sustainable use of biological diversity, such as indicator species; and (3) Described genomes and genes of social, scientific, or economic importance.

are held within a multilateral system that includes research centers, action plans, and the notion of facilitated access that is implemented through MTA [6 art. art. 14–17].

In Mexico there is one gene bank under the Consortium of International Agricultural Research Centers, the International Maize and Wheat Improvement Center, that provides breeders with basic selected lines or elite germplasm that allow for the development of new varieties around the world, this facility is devoted to maize and wheat and is under the Treaty on PGR for food and agriculture.

Mesoamerican PGR and Plant Breeder's Rights in Mexico

As a proxy to the real diversity of Mesoamerican PGR, we used a list of species domesticated, semidomesticated, and intensively managed plants of Mexico and Mesoamerica [31]: it includes 142 species of which 60 % are food plants, 10 % are ornamentals, 8 % spices, and below 5 % we find beverages, forage, living fences, and wood. Out of the 79 genera mentioned in this list, those with more species are *Agave* (12 spp.), *Opuntia* (8 spp.), and *Phaseolus* and *Leucaena* (5 spp. each); of the 43 families listed, those with more species are Fabaceae (18 spp.), Agavaceae (16 spp.), Cactaceae (15 spp.), and Asteraceae (10 spp.).

This list of Mesoamerican PGR was crossed with the species list of the Treaty on PGR for food and agriculture producing a list of plants considered of strategic worldwide importance classified as to their Mesoamerican origin: these species are thus under a "facilitated access" multilateral system. For the FAO in brief:

> Plant genetic resources for food and agriculture are crucial in feeding the world's population. They are the raw material that farmers and plant breeders use to improve the quality and productivity of our crops.

The annex I of the Treaty lists 64 crops: 35 are food crops and they include 33 genera: maize, rice, wheat, sorghum, millets in the Poaceae family; beans, pea, grass pea or lentil in the Fabaceae family. In the Forage category there are 29 crops and genera, mainly from Fabaceae and Poaceae families, and this will not be dealt with further.

This list was further trimmed using the criteria of existing plant breeder's rights applications in Mexico [8] and keeping only those for which there are commercial varieties being applied for under UPOV in Mexico. This final list provides then a proxy to the species that are currently of agricultural and agro-industrial interest in Mexico classified as being or not in the Treaty and as Mesoamerican in origin or not. The resulting list provides a contrast between the plants that are of Mesoamerican origin and those that are "important" for world food security and those are of current commercial value in the area. Table 22.6 provides a reference on the biological resources that are at stake for the Mesoamerican region as potential material for development of the regions exclusive resources but also as introduced proprietary material for agricultural and industrialization applications.

The PGR Treaty includes the Brassicaceae family with the greatest number of taxa, including rapeseed and others as such horseradish, cabbage, mustard, and

Table 22.6 Mesoamerican plant resources and crops in the multilateral system

Family, common name (botanical name)
Mesoamerican origin and in the Treaty
Fabaceae.
Beans (*Phaseolus*)
Poaceae
Maize (*Zea, Zea mays,* excluding *Zea perennis, Z. diploperennis,* and *Z. luxurians*)
In the Treaty non-mesoamerican origin
Fabaceae
Faba (*Cicer*)
Poaceae
Oat, barley, rice, sorghum, wheat (*Avena, Hordeum, Oryza, Sorghum, Triticum*)
Brassicaceae. Rapeseed (*Brassica*)
Rosaceae. Strawberry, Apple (*Fragaria, Malus*)
Solanaceae
Potato, Eggplant (*Solanum*)
Rutaceae. Citrus fruits (*Citrus*)
Arecaceae. Coconut (*Cocos*)
Apiaceae. Carrot (*Daucus*)
Musaceae. Banana (*Musa*)
Mesoamerican origin not in the treaty
Cactaceae. Nopal as vegetable, prickly pear and xoconostle (*Opuntia*)
Cucurbitaceae. Squash and chayote (*Cucurbita, Sechium*)
Solanaceae.
Tomato, green tomato, potato (*Lycopersicon esculentum, Physalis philadelphica*)
Annonaceae. Cherimola (*Annona*)
Amaranthaceae. Amaranth (*Amaranthus*)
Lauraceae. Avocado (*Persea*)
Myrtaceae. Guava (*Psidium*)
Caricaceae. Papaya (*Carica*)

Plant resources, Mesoamerican list from Perales et al. [31] and under access from the Annex I of ITPGR. Families are ordered in descending order of taxon richness according to a database integrating the plants included in both sources turnip. Apple and strawberry in the Rosacea family. In the potato family, we also find the eggplant (*Solanum*) which is not of Mesoamerican origin; other important crops considered in the treaty are families Rutaceae, Arecaceae, Apiaceae, and Musaceae.

Plant groups important to food and agriculture with Mesoamerican origin include the *Opuntia* cacti that produce nopal as vegetable and as prickly pear and *xoconostle* fruits. In wild form they are characteristic from semiarid areas, but as a commercial crop they are important in central Mexico. Squash, pumpkin, and chayote are cucurbitaceous crops that are commercially and culturally important in central Mexico. Agro-industrial tomatoes (*Lycopersicon*) are particularly important in Sonora, Michoacán, and Baja California. The "green or with hull tomato" (*Physalis*) is cultivated in Sinaloa, Michoacán, and Jalisco. Sinaloa, Sonora, and Nuevo León are the important potato growers in Mexico and they do so under industrial production. Avocado (*Persea*) is a Lauraceae and Mexico is an important world producer based primarily on the state of Michoacan that uses the Hass variety is the most exported by Mexico. Papaya (*Carica*) and bananas (Musaceae family) are also industrially produced. Marginally relevant crops include cherimola, Annonaceae family; amaranth (*Amaranthus*) to Amaranthaceae family; guava (*Psidium*) to Myrtaceae family.

Table 22.7 Industrial property, plant breeder's rights, and geographical indications

Industrial property in the Paris convention
Object
patents, utility models, industrial designs, trademarks, service marks, trade names, indications of source or appellations of origin, and the repression of unfair competition [1]
Understanding of industrial property
in the broadest sense and shall apply not only to industry and commerce proper, but likewise to agricultural and extractive industries and to all manufactured or natural products, for example, wines, grain, tobacco leaf, fruit, cattle, minerals, mineral waters, beer, flowers, and flour [1]
National treatment
as regards the protection of industrial property, enjoy in all the other countries of the Union the advantages that their respective laws now grant, or may hereafter grant, to nationals [2]
Plant Breeder's Rights in the UPOV Convention
Plant Variety:
a plant grouping contained within a single botanical taxon of the lowest known rank
Conditions of Protection:
Novelty, Distinctness; Uniformity and Stability
Breeder:
the person who bred, or discovered and developed, a variety
Geographical indications in the TRIPS Agreement
indications which identify a good as originating in the territory of a Member, or a region or locality in that territory, where a given quality, reputation or other characteristic of the good is essentially attributable to its geographical origin [22]

Comparative language between three policy global instruments: Paris Convention for the Protection of Industrial Property; International Convention for the Protection of New Plant Varieties (UPOV); and Agreement on Trade-Related Aspects of Intellectual Property Rights (TRIPS)

Table 22.7 provides basic concepts on the scope of industrial property, its national treatment principle and specifically plant breeder's rights. It shows that the Paris Convention creates a Union and its object is listed but not defined, a description of what should be understood as industrial property is given and the principle of national treatment that is neatly described. This is one of the cornerstones of industrial property and in general, of free trade agreements. Within this broad issue, we focus on plant breeder's rights and geographical indications because of their direct link to PGR.

According to a search made in April 2014 to the Plant Variety Database (PLUTO) at UPOV web site,[12] overall, at a regional level, we find that plant breeders rights applications (PBRA) in the USA has 37,639; while Canada has over 8163. Mexico has 1,492 applications and Colombia 984; while the rest of the Central American countries have none yet.[13] These data according to the Plant Variety Database (PLUTO) at UPOV web site.[14] Since 2001 the applications in Mexico have experimented an increase of 278 % from 395 [32] to 1 492 PBRA.

Table 22.8 shows that in Mexico 40 % of PBRA are for maize and beans, both in the Treaty and of Mesoamerican origin, while 25 % belong to 15 taxa with a Mesoamerican origin but are not in the Treaty. Finally, 35 % of the PBRA belong to 18 taxa in the Treaty. Maize alone has 22 % of the total of applications, is the crop that has more applications, but it is a lower proportion in relation to the 30 % reported in 1997 and 2001 [32]. Nowadays cotton is the second crop in number of applications but it means almost a fifth of maize, this is a big difference in the distribution of PBRA among species.

Mesoamerican food crops, except maize and bean, have only 68 PBRA and average of almost 3 by applicant that illustrates the low concentration of technological innovation between different actors. Maize has an average of 25 PBRA by applicant; although bean is a tenth of maize, it has almost an average of 6.4 applicants. Otherwise the number of applications of treaty food crops nonlocal in Mexico is four times bigger than the Mesoamerican crops, and has the double of average of applications by actor.

The data show a trend to develop technological innovation for the crops that are leading the world market of food in spite of the nutritional or potential food use of plants that have a more reduced cultural use, for example amaranth.

For selected Mesoamerican crops in Table 22.9, there were 480 applications for maize, cotton, bean, chili, chayote, and cabbage. Two crops which have the majority of applications, more than 81 %, are maize and cotton. Since 2001, cotton has experimented an increase of 100 % of applications and maize an increase of 180 % in the same period [32].

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[12] http://www.upov.org/pluto/en/

[13] As reference in other regions, there are 658 applications in China; 1031 in Chile; 3251 Brazil; 7033 South Africa; 13,695 Argentina; 27,722 in Japan; 31,620 in Germany; 39,299 USA; 48,831 Netherlands; and 53,765 France.

[14] http://www.upov.org/pluto/en/

Table 22.8 Plant breeder's rights applications in Mexico on the Treaty

		UPOV	
		812	130
Common name	Genus	Applications	Applicants
Mesoamerican plants/PGR Treaty		*359*	*18*
Food		*359*	*18*
Maize	*Zea*	327	13
Bean	*Phaseolus*	32	5
Mesoamerican plants not considered in PGR Treaty		*135*	*46*
Food		*68*	*24*
Avocado	*Persea*	17	5
Tomato[a]	*Lycopersicon*	19	4
Cabbage	*Cucurbita*	8	3
Guava	*Psidium*	6	2
Papaya	*Carica*	6	3
Amaranth	*Amaranthus*	3	1
Chayote	*Sechium*	3	1
Cactus pear	*Opuntia*	3	2
Green tomato	*Physalis*	2	2
Cherimoya	*Annona*	1	1
Other uses[b]		*67*	*22*
Cotton	*Gossypium*		9
Pepper (chili)	*Capsicum*	49	6
Marigold	*Tagetes*	14	3
Tabaquillo, tobacco	*Nicotiana*	3	3
Poinsettia	*Euphorbia*	1	1
Introduced crops considered in PGR Treaty		*318*	*66*
Food		*315*	*63*
Strawberry	*Fragaria*	103	13
Sorghum	*Sorghum*	60	6
Potato	*Solanum*	43	13
Wheat	*Tritricum*	34	5
Apple	*Malus*	17	8
Rice	*Oryza*	13	2
Wheat	*Triticum*	13	4
Rapeseed, Broccoli	*Brassica*	9	3
Lemon, Mandarine	*Citrus*	7	2
Chickpea	*Cicer*	5	1
Oats	*Avena*	4	1
Barley	*Hordeum*	4	2
Coconut	*Cocos*	1	1
Carrot	*Daucus*	1	1
Banana	*Musa*	1	1

(continued)

Table 22.8 (continued)

Common name	Genus	UPOV	
		812	130
		Applications	Applicants
Forage		*3*	*3*
Andropogon grass	*Andropogon*	1	1
Alfalfa	*Medicago*	1	1
Grass	*Poa*	1	1

Annex 1 of Treaty [6] was compared with the Mesoamerican plant resources and crop list [31], to differentiate Mesoamerican plants from Introduced crops. The main uses to this resources are food, forage and other like condiment, stimulant, fiber, ornamental and pigment. Number indicates applications and applicants to UPOV [8], sorted by source and use

[a]Genus: *Lycopersicon*, *Lycopersicum* and the sinonim *Solanum lycopersicum*

[b]Condiment, stimulant, fiber, ornamental, pigment

For maize, cotton, chilies, squash and chayote, a detailed analysis on concentration of PBRA and their distribution between public and private sector applicants is presented.

More than 68 % of the selected PBRA are maize, one of the most important grains in the world. Almost 61 % are varieties made by the private sector mainly two international enterprises: Monsanto (28 %) and Pioneer (33 %) and the public sector has 27 %, mainly INIFAP (25 %), that reflects a clear tendency to concentration.

Considering the economic relevance of maize for the world, is not a surprise the great number of applications, it means a lot of investment technological development.

The second crop is the cotton, a fundamental crop for the world textile industry. It is relevant that 95 % of all applications are in four companies D & PL Co, Monsanto, Bayer, and Cotton Seed. Maize and bean are considered in the ITPGR, but, unlike maize, bean has a little more than 6 % of the selected applications in Mexico and almost 90 % are made by the public sector despite FAO describes it as the most important food legume for direct consumption in the world: "beans are primarily a small-scale crop grown with few purchased inputs, subjected to biological, edaphic, and climatic problems."[15]

There are some crops that can be considered in a relevant level of trade, but not at the level and energetic contribution of maize. For example, all the types of chili represent 10 % of all PBRA. In the private sector Seminis Vegetable Seeds is the most relevant company, in the public sector INIFAP. On the other hand, the squash and chayote only have one application made by public sector. Chayote is a traditional crop not considering by ITPGR, yet is cultural and social relevant in Mexico.

Some crops have notably increased their applications: an example is the case of strawberry (*Fragaria* sp.) that has experimented an increasing of has 255 % since 2001 [32], passing from 29 to 103 PBRA in 2014 70 % of all were concentrated in

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[15] www.fao.org

Table 22.9 Selected crops and plant breeder's rights applications by sector in Mexico

Applicants with more than 1 % of all the PBRA	PBRA	Species	Average (PBRA / species)	% ($n = 1492$)
	1025			*68.7*
INIFAP	241	25	10	16.2
Monsanto	131	3	44	8.8
Pioneer Hi-Bred International	130	3	43	8.7
Driscoll Strawberry Associates	84	3	28	5.6
Seminis Vegetable Seeds	69	10	7	4.6
Rosen Tantau, Mathias Tantau Nachfolger	38	1	38	2.5
D & Pl Technology Holding Company	37	1	37	2.5
Florist de Kwakel	35	1	35	2.3
Meilland International	31	1	31	2.1
Meilland Star Rose	31	1	31	2.1
Jackson & Perkins Wholesale	30	1	30	2.0
Dow Agrosciences de México	26	1	26	1.7
Universidad Autónoma Chapingo (UACh)	25	20	1	1.7
Lux Riviera	22	1	22	1.5
The Regents of The University of California	21	4	5	1.4
Piet Schreurs Holding	20	2	10	1.3
Van Zanten Plants	20	2	10	1.3
Nunhems	19	6	3	1.3
De Ruiter's Nieuwe Rozen	15	1	15	1.0
National universities	*33*			*2.2*
Centro de Investigación Científica de Yucatán	10	2	5	0.7
Colegio de Postgraduados	12	3	4	0.8
Colegio Superior Agropecuario del Estado de Guerrero	1	1	1	0.1
Universidad Autónoma Agraria "Antonio Narro"	5	4	1	0.3
Universidad Autónoma de Chihuahua	1	1	1	0.1
Universidad Nacional Autónoma de México	3	3	1	0.2
Universidad Popular Autónoma del Estado de Puebla	1	1	1	0.1
International universities	*11*			*0.7*
Cornell University	2	1	2	0.1
North Carolina State University	1	1	1	0.1
Texas A & M University System	2	2	1	0.1
The Board of Regents of The University of Nebraska	1	1	1	0.1

(continued)

Table 22.9 (continued)

Applicants with more than 1 % of all the PBRA	PBRA	Species	Average (PBRA / species)	% ($n = 1492$)
	1025			*68.7*
The University of Florida Board of Trustees	4	1	4	0.3
Universidad de Córdoba	1	1	1	0.1

Considering a total 1492 UPOV Applications, according to the latest visit to the Plant variety database (PLUTO)

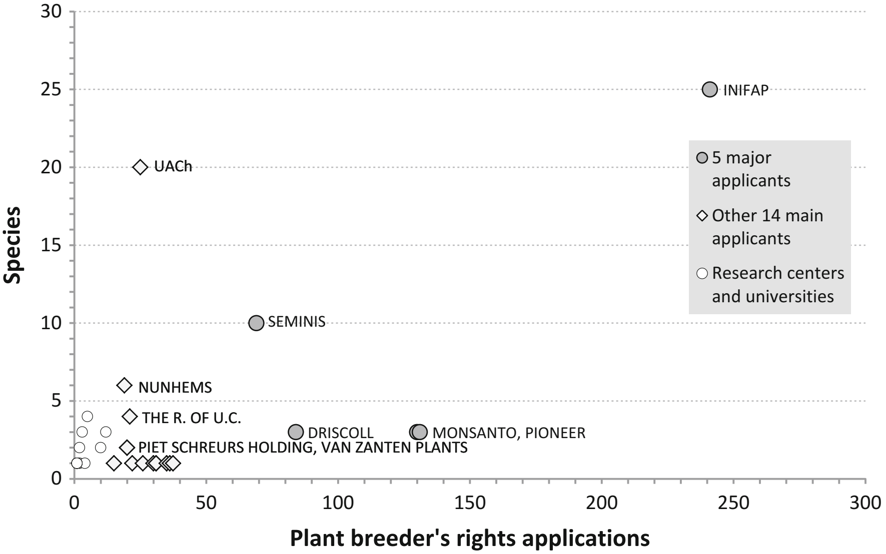

Fig. 22.2 Plant breeder's rights applicants, applications, and species diversity. This graphic is a resume from Table 22.9. It shows the relation between the number of species and applications of plant breeder's rights

two companies Driscoll (59) and the University of California [13]. *Rosa* sp., an ornamental crop, has increased in 155 % in 14 years, passing from 98 in 2001 [32] to 227 in 2014.

Sorghum has increased 172 % since 2001, passing from 22 to 60 in 2014. More than 80 % concentrated in only two companies Monsanto and Pioneer.

In Mexico, there are 19 companies that have more than 1 % of application each one, and all of them sum almost 68 % of all the applications. Among these, only INIFAP and Universidad Autonoma Chapingo (UACh) are Mexican public institutions, and there is only one foreign educational institution the Regents of the University of California (The R. of U.C.), all of the rest are private companies.

Forty-four per cent of all the applications are concentrated in four private companies, Seminis (4.6 %), Driscoll (5.6 %), Pioneer (8.7 %) and Monsanto (8.8 %), and one public Mexican institute INIFAP which has the greatest number of applications in Mexico (16.1 %), the double of the nearest private company. Applications of INIFAP have increased of 75 in 2001 [32] to 241 in 2014 that means 221 % in the last 13 years (Fig. 22.2).

The other 14 applicants are: De Ruiter's Nieuwe Rozen (1.2 %), Nunhems (1.3 %), Piet Schreurs Holding (1.3 %), Van Zanten Plants (1.3 %), The Regents Of The University Of California (1.3 %), Lux Riviera (1.5 %), Universidad Autónoma Chapingo (1.7 %), Dow Agrosciences (1.7 %), Jackson & Perkins Wholesale (2.0 %), Meilland International (2.0 %), Meilland Star Rose (2.0 %), Florist De Kwakel (2.4 %), D & Pl Technology Holding Company (2.5 %), Rosen Tantau, Mathias Tantau Nachfolger (2.6 %). Nine of all these applicants only have PBRA of one species.

INIFAP has 241 applications and 25 different species, UACh has 25 divides on 20 species, and these two public institutions are the most diversified in the number of species (Fig 22.2). The nearest private company is SEMINIS with 69 applications and ten species. On the other hand, the three main companies in number of PBRA have only three species each one. The public sector is working on a broader amount of crops, while the private sector is specialized in a number and type that is according to its commercial objective.

There are seven Mexican educational centers, universities, institutes, and centers of research except INIFAP and UACh, that just have 2.2 % of the PBRA in Mexico, and are more diversified respect of the species just 3 have 1 species, 1 of 2 species, 2 of 3, and 1 of 4. The international universities except the R. of U.C. the 1 %. Five of these six universities only have PBRA of 1 species and the other one 2 species.

The pedigrees of the lineages that are involved in PBR are not easy to trace. Thus, the extent to which CGIAR centers materials are the basis for the registered varieties is hard to asses. The centers produce elite or advanced lines that synthesize as much of the diversity contained in the seed bank so that breeders themselves can select for the characters of their interest, and they are distributed worldwide.

A Panorama of Geographical Indications from Canada to Colombia

Geographical indications are a form of industrial property that has been in the analysis of options for protection of some components of traditional knowledge and biological and genetic resources [33–35]. It took many years but finally geographical indications in the region are also in a highly dynamic process, and producers, rural development and agriculture departments are working on the differentiation of local and small producer products. The regional analysis reveals that there are over a hundred registered geographical indications related to biological resources, to origin, and to cultural and regional identities.

The idea is that local agriculture, food culture, and geographical indications are at the core of the French understanding of what is biodiversity and how it should be shared, paraphrasing the objective of the CBD that deals with access to genetic resources and benefit sharing, they write about the access to the benefits of sharing [33]. Thus, patenting varieties and biotechnological innovations are not the only possible way forward. The perspective of the commercial value of biodiversity as the only way in which "value" is created, contradicts the idea of creating public goods that are resources for communities. There are tension between a perspective of commercial uses of biodiversity and genetic resources [34] that focuses on fully fledged formal and industrial markets and a perspective that sees value in collective living heritages: local crops and products that sustain diverse agricultural practices and identities. The socioeconomics of GI and their role in trade are fundamental [35] and it relates to the strength of the link between the Geographical Indication, the biological resource and the regional and local culture varies widely [36].

Table 22.10 shows detail of the trends and patterns that can be seen throughout the region. In the USA, there is a growing understanding of European GI and their relationship to rural development [37]. They are now including collective or certification trademarks owned by local governments or indigenous peoples in Canada and the USA; the appellations of origin for spirits registered nationally in Mexico, Guatemala, and Nicaragua and included as geographical indications in specific Trade Agreements. We found a clear trend towards differentiation in coffee production, the development of Geographical Indication for handcrafts based on local raw materials and a growing trend to geographical differentiation of food products. The extent to which this includes PGR use and conservation is discussed because different Geographical Indications have conditions and increasing link between the sign and the landscape and culture [36].

A revision of this type of legal protection is difficult because there is no central database or register and the concepts vary widely. Looking for them carefully but not exhaustively we found 212 products with some protection from Canada to Colombia. Two-thirds of these are related to biological or genetic resources and this is the dataset that is described here.

Canada is particular because of its double identity. In Quebec it involves legal differences as well Francophone culture assume. Quebec Maple Syrup (maple, *Acer saccharum*), a geographical indication, has more than 13,000 producers, that produce 90 % of maple in the world. Planting maple is a form of cultivating forests and it is the largest business in the primary sector in Quebec. In Canada we found 12 geographical indications, all but one are associated to biological resources and almost a half are protected geographical indication (PGI). This country is the one with an agriculture specialty (AS). They have concurrent declarations of heritage for breeds or plant varieties that then support commercial strategies of the GI.

In USA, the protection policy is different; they have 14 marks with real or implied association to origin, for example "Indiana Grown." There are three principal groups state level; native American; and wins and spirit. Trademarks owned by state departments of agriculture based on the idea of differentiating state produce more, as well to specific brands of specific Indian nations, for example Red Lake Nation Foods, Inc. Red Lake, Minnesota (Red Lake Band of Chippewa Indians).

In Central America and Mexico is recognized the Denomination of Origin (DO) like a form to Geographical Indication. The coffee is the principal protect product

Table 22.10 An overview of geographical indications and biological resources in selected countries

Geographical indication	Product(s)	Biological resources	Product	GI type	Total
Canada					*12*
Quebec Maple Syrup	Maple	*Acer saccharum*	FA	GI	1
Maïs sucré de Neuville	Sweet corn	*Zea mays mays*	FA	PGI[a]	1
Agneau de Charlevoix	Lamb	*Ovis aries*	LV	PGI	1
Fromage de vache de race Canadienne	Cheese from heritage breed	*Bos taurus taurus*	LV	SA[a]	1
Volaille Chantecler de tradition	Chicken from heritage breed	*Gallus gallus domesticus*	LV	PGI[a]	1
Canadian Whisky and Rye Whisky	Grain and rye whisky	*Secale cereale cereale*	SW	GI	2
Cidre de glace du Québec	Apple cider	*Malus domestica*	SW	PGI[a]	1
Ontario Icewine, Vin de glace du Québec	Ice wine	*Vitis vinífera*	SW	PGI	2
Kwik'pak Fisheries (Yupik Eskimos)	Yukon River Keta (Chum) Salmon	*Oncorhynchus keta*	SF	TM	1
Select Nova Scotia	Fresh local produce and seafood	Local produce and seafood	SF / FA	CTM	1
United States of America					*66*
Grown, Preferred, Own, Pride, etc.	All rural products of the State	Various and with varying degree of specificity	FA	CTM	48
100 % Hawaii Coffee, Kona Coffee	Coffee	*Coffea* sp.	FA	GI	2
Florida Orange Juice	Orange juice	*Citrus* spp.	FA	CTM	1
Idaho Potato	Potato	*Solanum* sp.	FA	CTM	1
Lakota Sioux, South Dakota	Maize popcorn and bison jerky	*Zea mays* and *Bos bison*	FA	TM	1
Isleta Pueblo, New Mexico	Chili, Blue Corn and Anasazi Bean	*Capsicum* ssp., *Zea mays*, *Phaseolus* ssp.	FA	TM	1
Navajo Agricultural Products, New Mexico	Potatos, Corn, alfalfa, Beans, Barley, Wheat, Oats	*Solanum* sp., *Zea mays, Medicago sativa, Phaseolus* sp., *Hordeum* sp., *Triticum* sp., *Avena* sp.	FA	TM	1
Red Lake Nation, Minnesota	Wild Rice, Wild Fruits And Berries, Walleye Fish	*Oryza* sp. and others	FA	TM	1

(continued)

Table 22.10 (continued)

Geographical indication	Product(s)	Biological resources	Product	GI type	Total
Yakama Nation, Washington	Apple, Cherries, Pears, Peaches, Nectarines, Plums, Asparagus	*Malus* sp. and others	FA	TM	1
Lummi Nation, Washington	Seafood	Various	SF	TM	1
Swinomish Indian Tribe Community, Washington	Seafood	Various	SF	TM	1
Gros Ventre and Assiniboine Nations, Montana; Oglala Lakota, South Dakota	Buffalo	*Bos bison*	WL	TM	2
Brule Tribe, Kansas	Wild meats	Various	WL	TM	1
Yakama Nation, Washington	Huckelberries and Mushrooms	Various	WL	TM	1
Lumbee Tribe, North Carolina	Grape, apple, blackberry	*Vitis* sp., *Malus* sp., *Rubus* sp.	SW	TM	1
Kentucky Bourbon	Bourbon	*Zea mays* and other cereals	SW	GI	1
Tennessee Whiskey and Bourbon	Whiskey and bourbon	*Hordeum vulgare* and *Zea mays.* Other cereals like *Triticum* sp., *Secale cereale*	SW	GI	1
Mexico					*33*
Arroz de Morelos	Rice	*Oryza sativa*raza *indica*	FA	DO	1
Vainilla de Papantla	Vanilla	*Vanilla planifolia*	FA	DO	1
Café Chiapas, Café Veracruz	Coffee	*Coffea arabica*	FA	DO	2
Chile Habanero de la Península de Yucatán	Habanero chili	*Capsicum chinense*	FA	DO	1
Zachilos (Zacatecas)	Chili	*Capsicum* spp.	FA	CTM	1
Avo Mich. Aguacate Mexicano Región de Origen	Avocado	*Persea americana* var. Hass	FA	CTM	1
Guayava de Calvillo (Frutguay)	Guava	*Psidium guajava*	FA	CTM	1
La Labor (Estado de México), Zadux (Zacatecas)	Peach	*Prunus, P. pérsica*	FA	CTM	2
Mango Ataulfo del Soconusco Chiapas	Mango	*Mangifera caesia*	FA	DO	1
Naranja Montemorelos	Orange	*Citrus* spp.	FA	DO	1

(continued)

Table 22.10 (continued)

Geographical indication	Product(s)	Biological resources	Product	GI type	Total
Queso Cotija Región de Origen	Cheese	Native livestock	LV	CTM	1
Chakay-Langosta de las Reservas de Banco Chinchorro y Sian Kaan	Caribbean spiny lobster	*Panulirus argus*	SF	CTM	1
Certificado Venado Yucateco ACVY	Deer	*Odocoileus virginianus yucatanensis*	WL	CTM	1
Artesanía de coral negro Léemba Cozumel, Quintana Roo	Coral handcrafts	*Antiphates* sp.	WL	CTM	1
Charanda	Sugar cane spirit	*Saccharum officinarum*	SW	DO	1
Raicilla de Jalisco, Tenamaztle (Zacatecas)	Maguey spirit	*Agave inaequidens, Agave* spp.	SW	CTM	2
Sotol	Sotol spirit	*Dasylirion* spp.	SW	DO	1
Tequila, Mezcal, Bacanora	Maguey spirits	*Agave* spp.*, A. tequilana* var. azul, *A. angustifolia*	SW	DO	3
Artesanía de Papel Amate P'ete-i San Pablito Pahuatán	Paper from fibrous barks (Amate, ojite, tortocal, palo brujo, jonote, chichicaxtle and ortiga)	*Ficus* spp., *Brosimum alicastrum*, *Ulmus mexicana, Sapium oligoneuron, S. aucuparium, Trema micrantha, Urera caracasana, Myriocarpa cordifolia*	HC	CTM	1
Meyá-Che artesanía torneada Dzityá, Yucatán	Handcrafts from various tropical woods	Various	HC	CTM	1
Olinalá	Linaloe wood handcrafts	*Bursera linanoe*	HC	DO	1
Tallas de Madera Alebrijes Tonas de Oaxaca	Copal wood carvings	*Bursera* spp.	HC	CTM	1
Pasta de caña de maíz de J'atzingueni	Maize paste handcrafts	*Zea mays*	HC	CTM	1
Titlamatichichihua. Lacas de Temalacatzingo, Guerrero	Gourd, minerals, chia and axe	*Lagenaria, Salvia hispanica* and *Coccus* spp. (Hemiptera)	HC	CTM	1
Maque de Michoacán Región de Origen	Minerals, chia and axe	*Salvia hispanica* and *Coccus* spp. (Hemiptera)	HC	CTM	1

(continued)

Table 22.10 (continued)

Geographical indication	Product(s)	Biological resources	Product	GI type	Total
Mueble artesanal de Cuanajo	Pine wood handcrafts	*Pinus* spp.	HC	CTM	1
Mueble tallado de Pichátaro Región de origen	Pine wood handcrafts	*Pinus* spp.	HC	CTM	1
Silla de Opopeo Región de origen	Pine tree and royal palm	*Pinus spp./Sabal* spp.	HC	CTM	1
Guatemala					*3*
Café acatenango, Café Antigua	Coffee	*Coffea arábiga*	FA	DO	2
Ron de Guatemala	Rum	*Saccharum officinarum*	SW	DO	1
El Salvador					*1*
Café Apaneca-Ilamapetec	Coffee	*Coffea arábiga*	FA	DO	1
Honduras					*7*
Café Cagual, Café Camapara, Café Congolon, Café Erapuca, Café Guisayote, Café Marcala, Cafés del Occidente Hondureño	Coffee	*Coffea arábiga*	FA	GI	7
Nicaragua					*1*
Café de Nicaragua	Coffee	*Coffea arábiga*	FA	DO	1
Costa Rica					*4*
Banano de Costa Rica	Banana	*Musa* spp.	FA	GI	1
Café de Costa Rica	Coffee	*Coffea arábiga*	FA	GI	1
100 % Frijol de Costa Rica	Beans	*Phaseolus*	FA	CTM	1
Queso de Turrialba	Cheese	Livestock	LV	DO	1
Panama					*2*
Café de Palmira	Coffee	*Coffea arábiga*	FA	CTM	1
Piñas de la Chorrera	Pineapple	*Ananas comosus*	FA	CTM	1
Colombia					*23*
Bizcocho de Achira del Huila	Achira	*Canna edulis*	FA	DO	1
Café de Colombia, Café de Cauca, Café de Nariño	Coffee	*Coffea arábiga*	FA	DO	3
Cholupa del Huila	Cholupa or bone granadilla	*Passiflora maliformis*	FA	DO	1
Productos de las abejas de la Asoapiboy	Honey and pollen	*Apis mellifera*	FA	CTM	1

(continued)

Table 22.10 (continued)

Geographical indication	Product(s)	Biological resources	Product	GI type	Total
Cestería en Rollo de Guacamayas	Fique and reedgrass basketry	*Furcraea andina* y *Calamagrostis* sp.	FA	DO	1
Clavel, crisantemo y rosa de Colombia	Carnations, Chrisantemus and Rose	*Dianthus caryophyllus, Chrysanthemum* sp. *and Rosa* sp.	FA	DO	3
Quesos de Paipa y del Caquetá	Cheese	*Livestock*	FA	DO	2
Mopa Mopa Barniz de Pasto	Lackered wood	*Elaeagia pastoensis*	HC	DO	1
Sombrero Aguadeño, Sombrero Suazá, Sombreros de Sandoná	Iraca palm hats	*Carludovica palmata*	HC	DO	3
Tejeduría San Jacinto, Tejeduría Wayuu	Cotton weavings	*Gossypium* spp.	HC	DO	2
Tejeduría Zenú	Various fibers and natural colorants	*Gynerium sagittatum, Costus laevis, Citrus limon, Citrus aurantium, Caesalpinia coreacea, Genipa americana, Bixa orellana, Arrabidaea chica y Musa balbisiana*	HC	DO	1
Artesanías de Colosó	Iraca palm, plaintain fiber, plaintain, coconut palm braids, maize leaf and gourd scourer	*Carludovica palmata*, *Musa* spp., *Cocos* spp., *Zea mays*	HC	DO	1
Atuma	Chiqui-chiqui palm handcrafts	*Leopoldinia piassaba*	HC	DO	1
Palma estera del Cesar	Estera palm weavings	*Astrocaryum malibu*	HC	DO	1
Palo Sangre	Blood wood handcrafts	*Brosimum rubescens*	HC	DO	1

An overview of geographical indications and biological resources in Canada, USA, Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and Colombia shows difference between their intellectual property policies. For example, only in USA trademarks (TM) are the main form from protection, and in the other countries policy is Certification or collective trademarks (CTM). Number indicates the geographical indications totals for each category

Key to product category: *FA* Food and agriculture, *HC* Handcrafts, *LV* Livestock, *SF* Seafood, *WL* Wildlife, *SW* Spirits and wines

Key to GI type: *CTM* Certification or collective trademark, *DO* Denomination or Appellation of origin, *GI* Geographical indication, *PGI* Protected geographical indication, *SA* Agriculture specialty, *TM* Trademark in Guatemala, El Salvador, Nicaragua, Panama, and Colombia, and in every country there are one or more Geographic Indication associated to *Coffea arabiga*. Honduras has seven Denominations of Origin associated for this product.

Colombia has many products with some kind of geographic indication. In our list, 23 products, which only one is a collective trademark, the others are denominations of origin. The Handcrafts (basketry, hats, textile, and others) made with natural fibers have a very important place. There are three denominations of origin from coffee and other three to flowers: carnations, chrisantemus, and rose.

Mexico has 82 products with some kind of protection, 14 are Denomination of Origin and 68 collective trademark; almost a half is associated to biological resources. About the denominations of origin, *Arroz de Morelos* is grown in 22 towns in Morelos state and includes three registered rice varieties developed by INIFAP. *Naranja Montemorelos* is another Denomination of Origin from a town in Nuevo Leon state, in the north of Mexico. The spirits and wines with denomination of origin in Mexico are Charanda; *Raicilla de Jalisco*; Tenamaztle [mezcal from Nuevo León]; Tequila; Mezcal, and Bacanora. Bacanora is only from Sonora state and Mezcal is from Guerrero, Oaxaca, Durango, San Luis Potosí, and Zacatecas; the “Mezcal geographic corridor” in Michoacan state and the “Mezcal region” in Oaxaca. In Mexico, Michoacan is the state with more Certification or collective trademark in different kind of product. In the table we see several examples of their strategy. Other collective trademarks with geographic indication, in Mexico, are *Mi querencia*, *Tlayuda Oaxaqueña, a* maize product; *Fresa Michoacana Region de Origen* (strawberries); *Tierra Colorada* (beans, *Phaseolus*), a region in Guerrero state; Huamuchitos *Jamaica de Guerrero* (*Hibiscus flower*); *Limón Michoacano, Región de Origen* is a protected geographical region, has two species of lemons (*Citrus aurantiifolia* and *C. latifolia*); and Tampico onions (onions, *Allium cepa*).

Prickly pear fresh fruit and preserve are protected by five collective trademarks from Tamaulipas, Zacatecas, and Sonora. In the case of vanilla, in addition to appellation of origin, there are two collective trademarks, both from Veracruz.

Conclusions

ESC rights have been recognized in all countries of the region. We described the situation in terms of rights and policies that are being implemented by states and increasingly registered or demanded by individuals, groups, or collectivities.

The fact that PGRFA is essential for the future of humankind is recognized by all. How to best keep them diverse and available to communities is a more interesting question. The role of formal “protection,” “registration,” or “documentation” of PGR as heritage, as national resources, or as private intellectual property rights in these processes has been in debate for decades [38].

The current political, economic and social context could not be more complex, dynamic, and challenging: migration and human rights, food and agricultures, autonomies, culture and heritage, intellectual property, and free trade agreements.

However, the property, heritage and sovereignity vindications are on the move. Beyond research, things are happening in many areas that will have long lasting effects on biological and cultural resources. The outcomes of action, public and private, individual and collective will define what is inherited to the next generations.

The key question, perhaps: can PGR as public goods be preserved, protected or created in the contexts of cultural and natural heritage, through the sustainable use of biological resources articulated with softer industrial property such as PBR and GI? May they provide incentives to conservation or do they simply complicate, inhibit or prohibit seed interchange? [39, 40]. These questions remain in need of specific answers. The objectives of the heritage conventions are being met in the sense that states are taking action to protect heritage. There is a trend towards the glorification of the past but is there a genuine territorial strategy that respects the rights of local stakeholder while valuing this heritage. The principles and criteria of representativeness of the UNESCO process, signal that countries should go further, and that what is registered should represent humanities diverse heritages: in particular domestication and agricultural diversity as cultural processes linked to PGR and the viability of current rural livelihoods. The registration of agricultural landscapes and linguistic heritage are interesting innovations but they are only a part of what countries are doing. National, state, and local level heritage declarations are now quite common. How are they related to genetic resources in general and to PGRFA in particular? Bare in mind that historical agricultural and industrial landscape preservation but should not be immediately assumed to be preserving living agricultural landscapes and their intangible components.

The fact that the USA is not a member of the CBD and that Mexico is not a member of the PGR Treaty creates ambiguity in many legal issues and its consequences are important to PGR interchange, use, and preservation.

The comparative approach shows that the PGR of Mesoamerican cultures may provide countries and their agroinnovation institutions a relative comparative advantage in terms of privileged access to certain PGR. This opportunity should not distract focus protecting and providing the PGR that rural populations currently have or will need shortly and in the long term. Annex 1 of the PGR Treaty includes a highly reduced number of crops. It seems to focus on established world crops and not on the conservation, innovation, and development of the diversity of PGR for regional or national food and agricultural security.

In principle, heritage, resources and IPR law are used by the States' governments as a way to improve the economic competitive advantage of their countries. However, these laws tend to favor and attend to corporate private economic interests, which may hamper its collective purpose. Thus, the conservation of PGRFA becomes an issue of rights: social movements are transforming their heritage agenda since environmental heritage—natural or urban—is no longer seen as a sole governmental responsibility, but they understand that "without social mobilization the government will not link it to current and everyday needs of the population." [13, p 70].

Thus PGR conservation and use are linked to rights, individual and collective, in the context of biological and cultural innovation and social change. Food and hunger are at the core of human rights and lie together with agriculture and trade at all scales. Among the main policy objective, it is important to emphasize the viability of rural livelihoods, non-intellectual property rights (the right to say no), collective intellectual property, and intangible cultural heritage of humankind.

Rights are social and legal constructions that reflect values and obligations. For their fulfillment they require institutions that create the conditions for these rights to be a reality. The interested parties, the stakeholders, are individuals and communities, cultures as a whole: they are people with rights, individual and collective, organized or not. Collective legal actions to ensure that these rights are effectively respected and public goods created through research and conservation have been going on for years and will be necessary in decades to come. Meanwhile, we expect that this descriptive analysis contributes to this dialogue while the struggle is yet civil and politic. We stress the importance of applying a human rights approach to plant research and innovation that emphasizes local resources as natural and intangible cultural components. The effective rescue of heritage includes its collective and democratic appropriation: "the material and symbolic conditions needed so that all classes can share in it and find it significant" ([16 p70]).

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