

ETHNOBOTANY AND DOMESTICATION PROCESS OF *LEUCAENA* IN MEXICO.

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ABSTRACT.— This paper analyzes ethnobotanical information on the tropical tree legume genus *Leucaena* Benth. It is part of a taxonomical, archaeobotanical, ethnohistorical, and genetical study of the domestication process of these plants in Mexico. In general, uses are food and medicine; the wood is valued as fuel, for construction and for tool manufacturing. Young leaves, flower buds, immature legumes and seeds are eaten fresh, both raw and cooked; seeds are either dry-preserved whole and toasted or ground in a paste that is sun-dried and cooked; the bark is a vulnerary, the leaves and seeds are antiseptic and parasiticide. Within distribution ranges of taxa, local ethnic groups recognize and use natural populations, thus emphasizing the antiquity of this knowledge. Associated with this, there is variable cultural relevance of the taxa. Most important cultivated taxa are *L. esculenta* subsp. *esculenta* and *L. leucocephala* subsp. *glabrata*. The first is cultivated in central and southern Mexico, its biological area of origin and where it is extensively gathered, consumed and stored. The second is widespread under cultivation in warm to temperate zones, and probably originated in coastal southern Mexico. Some taxa have recently been introduced to management systems, which enhances variation of traditional management techniques.

Key words: ethnobotany; domestication process; *Leucaena*; Mexico.

RESUMEN.— Este artículo analiza la información etnobotánica disponible acerca del género de árboles tropicales *Leucaena* (Fabaceae, Mimosaceae), con énfasis en los taxa cultivados. Es parte de un estudio taxonómico, arqueobotánico, etnohistórico y genético del proceso de domesticación de estas plantas en México. Sus usos son como alimento y medicina, la madera sirve como leña, para construcción y para manufacturar utensilios. Las hojas, flores, legumbres y semillas inmaduras se comen frescas, crudas o cocinadas; las semillas se almacenan preparadas enteras -consumidas tostadas-, o molidas y secadas al sol -consumida cocinada-; la corteza es vulneraria; las hojas y semillas son antisépticas y parasitcidas. Dentro del ámbito de distribución de los taxa, las etnias locales reconocen y utilizan las poblaciones silvestres, indicando la antigüedad de este conocimiento. Asociado a esto existe variación en la importancia cultural de los taxa, siendo los más importantes en cultivo *L. esculenta* subsp. *esculenta* y *L. leucocephala* subsp. *glabrata*. La primera, cultivada en el centro y sur de México, su área de origen biológico, donde se recolecta extensivamente, se consume y almacena. La segunda es cultivada en las zonas cálidas a templadas del país, probablemente originaria de la costa sur de México. Algunos taxa han sido recientemente incorporados a sistemas tradicionales de manejo, incrementando la variabilidad de las formas de manejo tradicionales.

Palabras clave: Etnobotánica; proceso de domesticación; *Leucaena*; México.

RESUMÉ.— Cet article analyse l'information ethnobotanique disponible sur le genre des arbres tropicaux *Leucaena* (Fabaceae, Mimosaceae), en particulier sur les espèces cultivées au Mexique. L'étude fait partie d'une recherche taxonomique, archéobotanique, ethnohistorique et génétique, des processus de domestication de ces plantes au Mexique. Généralement, elles sont utilisées comme aliments et remèdes. Le bois sert à la construction, la fabrication d'outils, et comme combustible. Les feuilles, fleurs, gousses, graines, sont mangées à l'état jeune, crues ou cuites. Les graines sont stockées, simplement séchées (puis grillées au moment de la consommation), ou bien, moulues en galettes séchées au soleil (puis cuites dans un bouillon). L'écorce est vulnérable, les feuilles et les graines sont parasitocides et antiseptiques. Les différentes espèces étaient connues, nommées, et utilisées par chaque ethnie qui cohabitait avec elles, démontrant l'ancienneté de cette connaissance. Les espèces plus répandues sont *L. esculenta* subsp. *esculenta* et *L. leucocephala* subsp. *glabrata*. La première est cultivée au centre et au sud du Mexique (sa zone d'origine biologique) elle est récoltée extensivement, préparée et stockée. La seconde est cultivée dans les zones chaudes à tempérées du Mexique, probablement originaire de la côte sud. Récemment, quelques espèces ont été incorporées aux systèmes de culture traditionnels, occasionnant de nouvelles conduites de culture.

Mots clefs: Ethnobotanique, processus de domestication, *Leucaena*, Mexique.

INTRODUCTION

This paper analyzes the ethnobotanical information available for species of the genus *Leucaena* Benth. in Mexico. It is particularly directed to examining local people's knowledge of these legume trees, including classification, ecology, utilization and management, with emphasis on the cultivated taxa. It is part of a study of the domestication process of these plants (Zárate 1998), which also includes systematics (Zárate 1994), archaeobotany (Zárate 1999), ethnohistory (Zárate 1997) and genetics (Zárate 1999). The general aim of these studies is to contribute to the understanding of the origins and diffusion of traditional cultivated taxa, and of the evolution of the cultural counterpart of the *Leucaena* spp.-people interrelation. *Domestication.*— Domestication is a process occurring in an ethnobiological hyperspace; humans and plants interact, with each one of these entities having its particular and independent principles (e.g., culture and economy vs. genetics and ecology). Plants are an economic incentive needed for human subsistence; however, interaction between people and plants (and the ecosystem in general) occurs as a socially mediated process, which is driven by human work, i.e., management. Like all cultural processes, management evolves through the acquisition, transformation and transmission of information by social groups as part of their economic activities in an ecological context. Management -of both vegetation and each kind of plant- causes changes in both the plant's environment and the genetic structure of plant populations (i.e., evolution, which is analogous to ecotypic differentiation). The historical trends of the cultural aspects of the domestication process may be studied by comparison of ethnobotanical and historical aspects. This cultural sequence of change finds expression in genetic processes which become perceivable as taxonomical identity and morphological, ecological, and genetical variation.

The cultural context.—Mesoamerica has been a distinct center of civilization in which the use of natural resources is characterized by the exhaustive use of biological diversity and by a diverse spectrum of management intensity, both of the vegetation and of individual plant species (Caballero 1994; Casas *et al.* 1997). Thus a number of plant (and animal) taxa have been utilized in this area in conditions of diversified production which range from gathering to full domestication (Hernández-X. 1993), in close interaction with ecological and economic conditions. The results of this long history are a number of valuable and nowadays important crops, and a tradition of diversified ecological use of soil and vegetation (Bye 1993; Hernández-X. 1993). This is the context in which *Leucaena* spp. has been known, used and managed. Within this context, use of these trees as food is noteworthy because tender pods and seeds may be eaten uncooked. Other legume trees are consumed immature today, and maybe were more so in the past (Messer 1978; Felker 1981), but this is not frequent and trees are not cultivated nor extensively gathered. The fleshy legumes of mesquite (*Prosopis* spp.) are chewed to extract the sugar they contain, but seeds only become edible after being toasted and ground; so are seeds of other legume trees, such as *Lysiloma candida* and *Cercidium* spp. (Parra 1983). The soft edible pulp (arils) surrounding seeds of the genera of legume trees *Inga* and *Pithecelobium* are frequently consumed, gathered and commercialized, and the trees producing them are managed.

The appreciable consequences of the Spanish conquest on the ethnobotany of the genus are discussed elsewhere (Zárate 1997, 1998). The importance given by Mesoamerican cultures to *Leucaena* was mostly ignored by Europeans, and thus by the socio-economically dominant class. Because of this, traditional use and management of most taxa of *Leucaena* spp. underwent little acculturation, while partial cultural disjunction is observed in modern uses of some taxa (Zárate 1997, 1998).

Taxonomy and ecology.—According to Zárate (1994), the genus -in Fabaceae, Mimosaceae- comprises about 24 taxa of trees and shrubs -22 in Mexico; including 14 species and 18 subspecies, plus a number of little studied Central and South American taxa- in two sections, Sect. *Leucaena*, and Sect. *Macrophylla* Zárate. It is distributed from the Southern United States to Northern South America (Hughes 1998b). The taxa grow in different tropical environments, from arid to humid, forming part of a range of vegetation types including *matorrales*, low deciduous forests, sub-deciduous humid forests, gallery forests, mangrove edges, sandy shores, and road-side vegetation (Zárate 1994; Hughes 1993; Rzedowsky 1978). In humid environments, *Leucaena* taxa belong mostly to secondary vegetation, their dominance increasing with aridity. Most cultivated taxa belong to section *Leucaena*, characterized by having small leaflets (Zárate 1994).

A number of putative interspecific hybrids have been detected in *Leucaena*, some of which have been formally named (Zárate 1994; Hughes 1998a, 1998b; Hughes and Harris 1994). Some of the suspected hybrids seem to be a part of the biogeographical and genetic process of evolution in the genus, while others have been related to cultivation and human diffusion (Zárate 1994). Among these formally described hybrids, the only one that has been characterized beyond morphology is the hybrid between the *guaje rojo* and the *guaje verde*, *L. xmixtec*

Hughes et Harris (1994). This highly sterile tree has been found only where cultivation of the parental taxa is sympatric (Hughes and Harris 1994).

Ethnobotany.— Most taxa of *Leucaena* in Mexico are reported as edible by people, and some are gathered more or less intensely (Zárate 1994) (Appendix 1). The main cultigens are: the *guaje*¹ *rojo* or *guaje colorado*, “red *guaje*,” *L. esculenta* (Moc. et Sessé ex A. DC.) Benth., with two subspecies, *L. e.* subsp. *esculenta* and *L. e.* subsp. *paniculata* (Britton et Rose) Zárate (1994); and the *guaje verde*, “green *guaje*,” or *guaje blanco*, “white *guaje*”, *L. leucocephala* (Lam.) de Wit subsp. *glabrata* (Rose) Zárate (1987, 1994).

METHODS

Ethnobotanical information was obtained from diverse sources: literature (ethnographical and ethnobotanical), floristic studies, herbarium specimen labels—mainly from the Herbario Nacional de Mexico (MEXU). Field work provided information derived from open and structured interviews (Martin 1995), mainly during rapid surveys beginning in 1979 throughout most of the genus' distribution, and, in some areas, for longer periods (Papantla, Veracruz, 1988, 1993, 1997; Central Guerrero, 1979, 1981, 1984; Chapulco, Puebla: 1982-1984; Oaxaca, 1979-1981). Where possible, ethnographical works were compared with field data. Common names were recorded from literature, herbarium labels and field work. Established phonetic equivalencies were used when available. Transcription of field records followed Spanish phonetic approximations. Whenever possible, the identification of the plants corresponding to ethnobotanical data—i.e, names, uses, knowledge, management—was authenticated by the examination of plant material, vouchers of which were deposited in MEXU. Literature reports were compared with field data, when available. The taxa were identified following Zárate (1994). A comparative analysis was made of the ethnobotanical information thus compiled.

RESULTS AND DISCUSSION

Ethnographic studies of peoples of Mexico give information about the use of most taxa of *Leucaena*. The data range from detailed descriptions of uses to the mention of the plant's names. Field work confirmed the knowledge and uses of species of the genus by indigenous and mestizo groups throughout the country (Appendix 1). This knowledge is seemingly ancient and mostly shows a low degree of acculturation (Zárate 1997).

Local classifications.— Local people living in areas where one or more wild native taxa of *Leucaena* are found, have local names for them, some in native languages. Local people's perception of variation and identification of plants is, in general, precise and usually it agrees with taxonomic criteria. The exceptions to this statement seem to be due to lack of exploration, rather than to people's ignorance of the plants (Zárate 1994) (Appendix 1).

The better known folk classifications of *Leucaena* are the Nahuatl, Mixtec and

Zapotec (Messer 1978; Casas and Caballero 1996; Zárate 1997). The generic names in these languages are respectively, *uaxin*, *nduwa*, and *lya*, which are applied with modifiers to species and subspecies in the genus, and to legumes in other genera.

Within the area of cultivation of the *guaje rojo* and the *guaje verde* these are known by the Nahuatl-derived name *guaje*. A noticeable exception to this is in the Yucatan Peninsula where the putative Maya name for *L. l. leucocephala* is *uaxim* or *xaxim*, probably borrowed from the Nahuatl. Similar Nahuatl derivatives are *guash* in Puebla and Veracruz, and *guashe* in Chiapas, where *Leucaena* taxa are also named in non-Nahuatl local native languages. Some designations distinguish local native wild taxa from introductions by epithets denoting this. In Chiapas the native *guash de monte*, *L. collinsii* Britton et Rose subsp. *collinsii* (Zárate 1994), is distinguished from the *guash de Castilla*, *L. e. esculenta*.

Uses and parts used.— Use for food is consistent, except in a few cases in which it is mostly medicinal. In the Yucatan Peninsula the leaves of *uaxim* (*L. l. leucocephala*) are fed to chickens as a systemic ectoparasiticide to kill lice, and for other medicinal applications (Barrera et al. 1976; Martínez 1979). Also, in the Balsas River Basin *L. e.* subsp. *matudae* Zárate is not used as food but the bark is used as a remedy for witchcraft and as a vulnerary (Zárate 1994). Flower buds and young leaves of some taxa, and immature legumes and seeds of most taxa are eaten. The seeds, after being salt- or ash-cured and sun-dried, are known as *cacalas* or *guajesquite* - from Nahuatl *uaxizquitl* composed of *uaxin*, *guaje* and *izquitl*, toasted seeds (particularly, maize), derived from *icequi*, to toast something (Simèon 1977). In the native area of *L. e. esculenta*, *guajesquite*, derived mainly from wild trees, is prepared and commercialized. In Morelos, mature seeds gathered from wild trees of *L. macrophylla* Benth. subsp. *macrophylla* are likewise consumed (Zárate 1994). In Baja California Sur, the immature legumes of *L. lanceolata* S. Watson subsp. *lanceolata* are eaten raw, while dry seeds are eaten after being toasted and ground (Parra 1983). The galls produced by insects on the developing legumes of *L. e. esculenta*, called *bolochocos* or *polochocos*, are eaten raw in combination with other foods, such as beans (Messer 1978, Vázquez 1986, Casas et al. 1987, Zárate 1994; Casas and Caballero 1996) (Appendix 1).

Culinary tradition includes several recipes, the most relevant being the *guaxmole* -from Nahuatl, *uaxmolli*, composed of *uaxin* and *molli*, stew (Simèon 1977)- prepared with pork, beef or goat meat. Several kinds of sauces (*salsa de guajes*) are made with or without chili peppers, sometimes including tomato, onion and spices, usually with garlic. The *tortas de guaje* is a "guaje omelet" made with immature seeds beaten with egg and cheese, and fried on a pan. *Guajesquite* is washed and drained, toasted on a flat metal or earthenware pan (*comal*) until they burst like popcorn, and eaten in *tacos* with chili pepper sauces, or alone adding lemon juice, salt and powdered chili pepper (Kennedy 1992). In the Tehuacan Valley, Puebla, during the season when goats are sacrificed (*matanza*), *guaje rojo* seeds are cooked with their meat (Paredes-Colín 1977). In this region, *guaxmole* is flavored with avocado leaves (*Persea americana* Mill.).

In general, when *Leucaena* spp. products are used for food they supplement the diet, due to its content in some important vitamins -and perhaps minerals too (Kelly and Palerm 1952). While this may be valid for most cases, *L. e. esculenta* is

sometimes more important in the diet, supplying protein. Such is the case of the elaborate products which may be stored (the *guajesquite* and the "bread" described below). This alimentary pattern corresponds with a strategy based on main staple foodstuffs, usually crop species, supplemented with seasonally available foods that are frequently gathered.

The wood is used as firewood, and that of *L. esculenta* is used by the Popoloca in Puebla for house construction (Jäcklein 1974). Utensils and tools are also reportedly made from the wood of *L. lanceolata* cultivated by the Huaves (Zizumbo and Colunga 1982). Similar uses and properties of wood of *Leucaena* spp. are known from documents of the sixteenth century (Zárate 1997).

Medicinal uses are also common and widespread. In general, leaves and seeds of these plants are used to fight infections both of the digestive and of the respiratory systems. Topical use of the ground bark of all three subspecies of *L. esculenta* (Zárate 1994) (sometimes mixed with honey) is recommended for infected wounds (vulnerary). The seeds of these last named taxa are considered an eupeptic and aphrodisiac (Díaz 1976, Hernández 1960). In the original illustration of "*Mimosa esculenta*" (slide no. 6331-627, Hunt Institute for Botanical Documentation), which forms part of the *Iconografía de la Flora Mexicana* compiled by Sessé and Mociño (1887, 1893), both the edibility and the aphrodisiac properties of *L. esculenta* subsp. *esculenta* are mentioned. The bark of *L. e. matudae* is used in magic medicine for treatment of witchcraft, which is associated with the Nahuatl invocation repeated in silence by the healer when gathering, preparing, giving the remedy to the patient, and ending the ritual. *Leucaena c. collinsii* from Chiapas is reported as antirheumatic (Díaz 1976) (Appendix 1).

These medicinal uses contrast with reports of toxicity of the leaves, seeds and pods for cattle, a fact already known by Spanish conquerors (Zárate 1997): When eaten, it causes hair-loss and, in ruminants, goiter. The responsible of this effect is the mildly toxic amino acid mimosine, which in ruminants is degraded to the potent goiterogen 3-hydroxy-4-1H pyridone (DHP). Toxic effects in ruminants may be avoided by inoculating cattle with the bacteria *Synergistes jonesii*, which is capable of degrading DHP (Jones and Megarrity 1986). Biological activity of mimosine in animal cells has been attributed to the decondensation of chromatin and nucleolar fibrillar component (Vogt 1991). This highly specific protein synthesis inhibition may explain the loss of hair and the reported properties against infections and a broad range of parasites. This fact suggests that *Leucaena* spp. could have potential in the treatment of tumors.

Economic importance.— Commercialization of products of several species of *Leucaena* is common in markets of many parts of Central Mexico. Among these markets are local weekly and daily marketplaces as well as established markets. In markets, *guajes* are sold in permanent stalls and by temporal vendors. In the main supply centers in Mexico City, *guajes* are traded in large scale by specialized merchants called *acaparadores*, who buy *guajes* from local producers. In this and other large towns and cities *guajes* are usually offered together with ethnic plant and animal foodstuffs. Less frequently, they may be found along with more common vegetables such as potatoes, carrots, celery, tomatoes, and so on. More rarely, *guajes* are sold in supermarkets.

The legumes of the short day plant *L. e. esculenta*, and those of *L. e. paniculata* which mature during the rainy season, are replaced during most part of the year by *L. l. glabrata*, which produces legumes all year round, as long as water is provided. Regionally (State of Mexico), the legumes of *L. m. macrophylla* are offered; so are the leaves, pod galls (*bolochocos*) and dry seeds of *L. esculenta* (*guajesquite*) (Guerrero, Morelos and Puebla); the fresh legumes of *L. cuspidata* Standley are sold in the weekly market of Ixmiquilpan, Hidalgo, during the production season (September). Legumes of *L. confertiflora* Zárate subsp. *adenotheloidea* Zárate (1994), both cultivated and gathered wild at Chapulco, Puebla, and nearby locations, are commercialized in local markets in the area of the Tehuacan Valley. Products in the market come mainly from cultivated populations, but may also have wild or somewhat managed provenance. In the first case are all instances of *L. l. glabrata*, and most examples of sale of *L. esculenta* and *L. c. adenotheloidea*. Wild provenance is dominant in commercialized products of *L. macrophylla* and *L. cuspidata*. *Guajesquite* made from *L. e. esculenta* is mainly from wild trees, although there is evidence of a possibly long history of management of some apparently wild populations (Casas and Caballero 1996). Legumes of *L. c. adenotheloidea* in markets come from both cultivated and wild trees. Most taxa are known to be considered edible and are gathered from wild or somewhat altered populations (Appendix 1).

Leucaena esculenta.— This species is native to the Balsas River Basin at elevations from 850 to 2200 m above sea level, it is found cultivated in this area and in Central Mexico, in Zacatecas, Jalisco, Hidalgo, Puebla, Veracruz, Michoacán, México, Guerrero, Morelos, Oaxaca and Chiapas (Zárate 1994:132, figure 6). Outside this area it is occasionally found cultivated. The subspecies *esculenta* is common in the northern and western part of the distribution, whereas the subspecies *paniculata* is found at higher altitudes in Zacatecas, Puebla, Guerrero, Morelos and Oaxaca. In Oaxaca, the characteristics distinguishing subspecies *esculenta* and *paniculata* -respectively, angled branches and red flowers vs. terete branches and reddish flowers, among others- are frequently combined in cultivated individual trees. Local wild populations of *L. e. paniculata* do not have such mixed characteristics (Zárate 1994). This may be due to hybridization between both subspecies, aided by the above mentioned overlap in phenology, as suggested by the polyploidy of these southern populations of the *guaje rojo*. Archaeobotanical evidence supports that such hybridization would have derived from the diffusion of *L. e. esculenta* to areas with native *L. e. paniculata* populations (Zárate 1994). Subspecies *paniculata* is sometimes cultivated, particularly in the margins of the distribution of subspecies *esculenta*, at or above 2000 m, in the states of Morelos, Puebla and Oaxaca. Subspecies *matudae*, is endemic to the Central Balsas Basin area, and has not been seen cultivated (Zárate 1994).

The *guaje rojo* is gathered from wild and managed trees for consumption of the fresh (green) seeds, which are eaten raw or cooked. The reddish legumes -tied up in bundles- are sold in markets in many parts of Mexico. Subspecies *esculenta* is deciduous, flowering while leafless -an adaptation of tropical dry tropical forest trees. Legumes of most highly prized *L. e.* subsp. *esculenta* trees (*hueyuaxin*) mature in the spring, while other populations -having lower quality- mature later. Thus, the legumes of *guaje rojo* are available from August to March. Subspecies

paniculata matures during the summer and fall. The Valley Zapotec from Mitla, Oaxaca, take advantage of both subspecies, recognizing them as *lya gusghi* (*lya*, Valley Zapotec generic name, and *gusghi*, rainy season; "rainy season *guaje*") and *lya kures* (similarly, "dry season *guaje*") (Messer 1978; Zárate 1994).

Within the heartland of the *guaje rojo*, in the Cañada Region of Guerrero, the seeds of subsp. *esculenta* are extensively gathered from wild and managed populations to be prepared as *guajesquite* which may be stored for further use. It is sold in local markets (e.g., Iguala and Huamuxtitlán, Guerrero and Cuernavaca, Morelos) by seed merchants. Within this area, another form of storable preparation is known: the fresh seeds are ground into a bread-like cake and stored wrapped in plastic after being sun-dried. This preparation is consumed in stew-like dishes, with or without meat. According to Casas and Caballero (1996), these two preparations are the only wild food resources stored by the Mixtec people in Guerrero. This "guaje bread" may be the same as that noticed during the sixteenth century by Hernández (1960; Zárate 1997).

Management.— These trees (both subspecies) are managed in various agricultural systems, grading in intensity, including *in situ* selection of *L. e. esculenta* in sites under fallow cultivation in dry tropical forests (Casas and Caballero 1996), home gardens, and in high density pure stands. Frequently, it is planted along water channels (*apantles*) and in furrow ridges between *milpas* (*bordos*). Vegetative propagation is not practiced for any species of the genus which are always seed-propagated, commonly by direct planting, but they can also be transplanted. In some cases, the presence of a seedbank makes planting unnecessary.

Diffusion.— Cultigens of the species seem to have been dispersed from some parts of the Balsas Basin to all parts of the range of cultivation. Some places of origin of cultigens known today are the upper valleys of Morelos (Cuernavaca and surrounding areas), an area in the State of Mexico (Temascaltepec area), and the Tierra Caliente region of Guerrero and Michoacán (Teloloapan, Guerrero-Tiquicheo, Michoacán area); these are all regions where Nahuatl is spoken.

Leucaena leucocephala.— Subspecies *leucocephala* is native along the Caribbean Coast of Mexico, the Antilles, and Florida, while the subspecies *glabrata* is widespread in Mexico, but its native area is not completely certain (see below) (Zárate 1987, 1994). The subspecies *glabrata* is cultivated and has recently been dispersed as a weed. While being typical of humid tropical environments, in cultivation it has a broad ecological range. A cultigen initially identified as subspecies *leucocephala* (Zárate 1987, 1994) is known cultivated by the Coast Totonac of Veracruz, and by the Totonac and the Nahua from the Sierra Norte de Puebla region (Zárate 1987, 1994). However, the identity of this plant is questionable, and it is likely that it is a hybrid of the subspecies *glabrata* and *L. pulverulenta*. In the Maya area, the native *L. l. leucocephala* is part of home gardens (Barrera 1980; Rico-Gray *et al.* 1990).

Management. In the Totonac region subspecies *glabrata* is managed in slash and burn milpas, acahuals (managed secondary vegetation) and in managed pastures (Kelly and Palerm 1952; Medellín 1990); elsewhere, within its distribution range, it is mainly found in patios, homegardens and in pure stands (Lazos *et al.* 1988; Zárate 1994). Its establishment and production seem to depend largely on irrigation. In Jalcomulco, Veracruz, pure stands of *L. l. glabrata* are grown on the

Jalcomulco River banks, apparently forming spontaneous hybrids with the native taxon *L. diversifolia* (Schldl.) Benth. subsp. *diversifolia* (Zárate 1994).

Diffusion. This species colonized the tropics of the world through European introduction via the Philippines (Zárate 1987, 1997, 1998). However, the aggressive subspecies *leucocephala* has become a problem for some countries, leading to the introduction of the more useful subspecies *glabrata* (Dijkman 1950, Anonymous 1984, Hughes 1993). This trend has reached Mexico, where importation of germplasm is occurring even today.

Cultigens of subspecies *glabrata* probably originated along rivers in the Sierra Madre del Sur or along the southern Pacific Coast of Mexico. From here, it reached its present area of traditional cultivation along Michoacán, Guerrero, Morelos, Puebla and Oaxaca. Archaeological evidence suggests that *L. l. glabrata* was introduced to the Tehuacan Valley during the Classic period (Palo Blanco phase), and perhaps to the Gulf of Mexico area, and that it was associated with irrigation agriculture (Zárate 1998). The cultivation of *L. l. glabrata* occurs where water is available and low temperatures do not limit its growth. Conversely, however, cultivation of *L. esculenta* does not occur at low elevations and may be damaged by excessive humidity (Zárate 1994).

Other cultivated taxa.— Other taxa are cultivated in lower degree, including some newly introduced cultigens and others that seem traditional. In the first case, the *guaje zacatzin*, *L. c. adonotheloidea* is a small, multiple-stemmed tree cultivated at 1800-2000 m above sea level in Chapulco, Puebla (Zárate 1984, 1994). The ethnobotanical evidence indicates that this shrubby tree was initially planted at the beginning of the present century. It is grown in home gardens with other trees in borders limiting the corn fields (*milpas*). Native populations exist in the neighboring Sierra de Zongolica, where it has traditionally been gathered for consumption, trade and sale (Zárate 1994). Irrigation seems to be causing the preference of the *guaje zacatzin* over the older cultigens of the *guaje colorado* (*L. e paniculata*), because the latter is damaged by constant moisture while the first responds with luscious growth and abundant legume production (Zárate 1994).

In the same case is *L. cuspidata* Standley, a small tree from arid vegetation in San Luis Potosí, Querétaro and Hidalgo (Zárate 1994), of incipient cultivation at the Mezquital Valley (Hughes 1993). As a tradition, the Otomi people gathered this shrub's legumes (Zárate 1994) and currently are turning to its cultivation.

Of unknown antiquity in cultivation, *L. lanceolata* -belonging to *Leucaena* Section *Macrophylla* Zárate (1994)- is grown in live fences for fodder by the Huaves of San Mateo del Mar, Oaxaca (Zizumbo and Colunga 1982).

Two other taxa are grown in living fences in Southern Mexico: *L. c. collinsii*, and *L. shannonii* J. D. Smith subsp. *shannonii*. Both taxa are of Central American affinity and are Mexican subspecies (Zárate 1994) disjunct from other subspecies in Central America (Hughes 1993). Precise antiquity of their cultivation is unknown.

Management and agricultural systems.— Physical factors such as climate, soil and vegetation influence the decision about which taxa to cultivate, but the choice is also influenced by cultural factors. The degree of intention and the effectiveness of the various managed systems known for *Leucaena* spp. ranges from individual

selection of trees *in situ* (without planting)—*L. e. esculenta* (Casas and Caballero 1996), and *L. l. leucocephala* (Kelly and Palerm 1952; Medellín 1990; Zárate 1994); the favoring and encouragement of volunteer recruits in culture—*L. e. paniculata*. in Chapulco, Puebla (Zárate 1994); to, the planting of seeds either directly to the fields—*L. e. esculenta* (Casas and Caballero 1996), *L. l. glabrata*, and *L. c. adenotheleidea*—or *ex situ* to be transplanted—*L. c. adenotheleidea* (Zárate 1994).

CONCLUSIONS

Relative importance of taxa.— From the data presented here, and from the ethnohistorical analysis (Zárate 1997), it may be concluded that the taxon with most ethnobotanical relevance in Mexico is *L. e. esculenta*, followed in order of importance by *L. l. glabrata*. The native area of *L. e. esculenta* has been approximately outlined, also it has been determined that the highly prized cultigens of this species (the *hueyuaxin*) originate in the higher portions along the northern border of this region.

The geographic origin of *L. l. glabrata* and of its cultivation is less certain. Most probably, the taxon is native along the rivers draining from the Mexican Pacific slopes. As mentioned, the reviewed archaeological evidence suggests that this cultigen did not originate in the Gulf of Mexico area; rather, it was likely introduced to Eastern Mexico from some place within the Balsas Basin area during the Classic period. However, *L. l. leucocephala* seems native to the Yucatan Peninsula and across the Tehuantepec Isthmus (Zárate 1994).

A Central American cultivation area is recognized which is characterized by management in living fences of native taxa. Mexican subspecies of *L. collinsii* and *L. shannonii* (Zárate 1994) are cultivated in the northern portion of this area extending into Guatemala (Hughes 1993, 1998b). The tradition associated with this area seems to be independent from those in the Balsas River Basin and Gulf of Mexico regions. History of migrations of the Pipil Nicarao (Fowler 1989) could have influenced this cultivation tradition, but that is uncertain. While *L. esculenta* did not diffuse beyond Mexico, knowledge of the genus did: the Pipil language from El Salvador records the word *wa:xin*, plural, *wahwa:xin*, meaning *guaje* tree (Campbell 1985).

Ethnobotanical evidence and the domestication of Leucaena.— A model for the process of domestication of the taxa in *Leucaena* has been proposed on a multidisciplinary basis, of which this study forms part (Zárate 1998, 1999). A genetic analysis made of putative isozyme genes of samples from the same wild and *in situ* selected populations morphologically studied by Casas and Caballero (1996), agrees with the differentiation observed by these authors in those characteristics of the fruit which are selected by people (Zárate 1999). This genetic evidence (Zárate 1999), together with inferences coming from phytogeography (distribution of populations) (Zárate 1994), ethnohistory (Zárate 1997), archaeobotany (Zárate 1999), and morphology (Zárate 1994; Casas and Caballero 1996), also suggests that domestication of *L. e. esculenta* must have proceeded, in part, by a form of management similar to that observed by Casas and Caballero (1996), acting during prolonged periods of time,

and over selected ecotypes. This form of selection acts upon locally available variation but is strengthened by diffusion of trees, which have themselves been selected along a historical process acting extensively upon the species' ecological and geographic milieus (Zárate 1999).

The ethnobotany of the genus in Mexico uncovers a geographic mosaic of taxacultures composed of wild, native taxa, in areas where local people gather and know each one as part of their knowledge of the environment. Overlapped with this pattern, some taxa are mostly found under more intense forms of management, and genetic variation present is apparently more or less determined by the history of such management. These facts may be observed as ethnobotanical manifestations: people recognize and appraise the quality of their plants, and of those from the region and beyond. Accordingly, people make attempts to improve the quality of their plantings either by introducing genetic material (seeds in this case), by elimination and favoring of present trees, or by a combination of both. Thus land race populations in areas where these were introduced are usually accompanied by introduced, higher quality cultigens. The distribution of these prized cultigens aids in charting their provenance and diffusion patterns.

Culturally, this situation in which a few taxa are widespread and cultivated, while other are gathered and relevant only at a local scale, is a consequence of the historical interaction between economic tradition, species distribution, ecological importance, and relative importance of cultural groups. There is a noticeable cultural identity of the most relevant taxa, their uses and their management by Nahuatl speakers in Central Mexico. The magic-medicinal use of *L. e. matudae* mentioned above is an important geographical and cultural indicator because it matches with the area of major alimentary relevance of the *guajes*, and because it provides cultural identity clues. The context of the use of this magic medicine is similar in many respects to that described by Aguirre-Beltrán (1992) for *Olloloqui* (*Ipomoea corimbosa*). In general, such similarities include invocation, ritual performance, participants attitudes, patient motivations and effects of treatment.

Other clues come from: sixteen century accounts of its importance for Nahuatl speakers (Zárate 1987); phytogeography (Zárate 1994); and, previously discussed archaeological evidence of diffusion of *L. e. esculenta* to neighboring Mixtec and Zapotec peoples (Zárate 1999). Also, evidence of diffusion of *L. l. glabrata* to the Tehuacan Valley, putatively with irrigation, has been associated with Nahuatl or Mixtec speakers on the basis of ceramic findings (MacNeish et al., 1970).

The cultivation of the *guaje verde* is, in general, associated with that of *L. e. esculenta* in the areas where both exist. However due to ecological conditions, *L. l. glabrata* is cultivated in places where the *guaje rojo* would not grow, areas which include many ethnic groups besides Nahuatl speakers. The Nahua identity of this species is weaker than that of *L. e. esculenta*. It seems to have been of relatively secondary importance to the sixteenth century Nahuatl speakers (Zárate 1997), yet its diffusion could have been also associated with these ethnic groups, as suggested by archaeology (Zárate 1998). All this indicates that Nahuatl speakers have been the main diffusers of the knowledge, use and cultivation of *L. e. esculenta* and *L. l. glabrata*. It remains to be seen whether ancient gatherers of *guaje rojo* seeds were actually Nahuatl speakers, since when they did this and whether they learned this from other people are questions that may only be answered by archaeology.

New domestication processes and production systems are being generated for trees and shrubs of the genus *Leucaena* in Mexico, apparently even faster than the promotion of the "modernized" uses, i.e. those praised by some international researchers who are sometimes largely ignorant of traditional uses in Mexico. This brings about incipient domestication of taxa formerly gathered from the wild. In this last instance there are at least two taxa, both from dry environments: *L. cuspidata* in the Mezquital Valley, and *L. c. adenotheleidea* near the Tehuacan Valley. In the former case, innovation is observed as variation in the management techniques used, a diversification which contrasts with more or less fixed traditional management of previously established cultigens in the same place.

NOTES

¹ The Spanish name *guaje* is derived from the Nahuatl *uaxin*, which is the generic name for *Leucaena* trees; it is also applied to the legumes and to *L. e. esculenta* (Siméon 1977; Zárate 1997). Nahuatl derivatives are known, such as *uaxin chichiltic* "red guaje", *calluaxin* "house guaje", etc. Some of these names apply to other genera, such as *tepeuaxin* (*Lysiloma* spp.). Gloss variations are found in sixteen century documents: *uaxi*, *hoaxin*, *-huaxin*, *-oaxin* (Zárate 1997).

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LITERATURE CITED

- ANONYMOUS. 1984. *Leucaena*: Promising forage and tree crop for the tropics. National Academy of Sciences, Washington, D.C.
- AGUIRRE-BELTRÁN, G. 1992. *Obra Antropológica. VIII. Medicina y Magia: El Proceso de Aculturación en la Estructura Colonial*. Universidad Veracruzana. Instituto Nacional Indigenista. Gobierno del Estado de Veracruz. Fondo de Cultura Económica. pp.126-133.
- ALCORN, J. 1984. *Huastec Mayan Ethnobotany*. University of Texas Press, Austin.
- BARRERA, A. 1980. Sobre la unidad de habitación tradicional campesina y el manejo de los recursos bióticos en el área maya yucatanense. I. Árboles y arbustos de los huertos familiares. *Biótica* 5 (3):115-128.
- , A.V. BARRERA and R.M. LÓPEZ-FRANCO. 1976. *Nomenclatura etnobotánica Maya. Una interpretación taxonómica*. Instituto Nacional de Antropología e Historia. Colección Científica. Etnología. No. 36. Mexico City.
- BYE, R. 1993. The role of humans in the diversification of plants in Mexico. Pp. 707-731 in T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, (editors). *Biological Diversity of Mexico*. Oxford University Press, N.Y.

- CABALLERO, J. 1994. La dimension culturelle de la diversité végétale au Mexique. *Journal D'Agriculture Traditionnelle et de Botanique Appliquee*, Nouvelle Série 36:145-158.
- CAMPBELL, L. 1985. *The Pipil Language of El Salvador*. Mouton Publishers, New York.
- CASAS, A. 1992. Etnobotánica y procesos de domesticación en *Leucaena esculenta* (Moc. et Sessé ex A. DC.) Benth. M. Sc. thesis. Facultad de Ciencias. Universidad Nacional Autónoma de México, Mexico City.
- , and J. CABALLERO. 1996. Traditional management and morphological variation in *Leucaena esculenta* (Fabaceae: Mimosoideae) in the Mixtec Region of Guerrero, Mexico. *Economic Botany* 50(2):167-181.
- , J.L. VIVEROS, E. KATZ and J. CABALLERO. 1987. Las plantas en la alimentación Mixteca: una aproximación etnobotánica. *América Indígena* 47 (2):317-343.
- , ———, and J. CABALLERO. 1994. Etnobotánica mixteca: Sociedad, cultura y recursos naturales en La Montaña, Guerrero. Colección Presencias. Consejo Nacional para la Cultura y las Artes. Instituto Nacional Indigenista, Mexico City.
- , J. CABALLERO, C. MAPES and S. ZÁRATE. 1997. Manejo de la vegetación, domesticación de plantas y origen de la agricultura en Mesoamérica. *Boletín de la Sociedad Botánica de México* 61:31-47.
- DÍAZ, J. L. 1976. Índices y Sinonímias de las Plantas Medicinales de Mexico. Monografías Científicas. Instituto Mexicano para el Estudio de las Plantas Medicinales, A. C., Mexico City.
- DIJKMAN, M. 1950. *Leucaena* a promising soil erosion control plant. *Economic Botany* 4:337-349.
- FELKER, P. 1981. Uses of tree legumes in semiarid regions. *Economic Botany* 35:174-186.
- FOWLER, W. R. 1989. The cultural evolution of ancient Nahua civilization. Pipil-Nicarao of Central America. The civilization of the American Indians, volume 194. University of Oklahoma Press.
- GONZÁLEZ-ORTEGA, J. 1929. *Catálogo Sistemático de las Plantas de Sinaloa*. Imprenta de la Escuela Preparatoria, Mazatlán.
- HERNÁNDEZ, F. 1960. *Obras Completas*. Tomo II. Historia natural de Nueva España, volume I. Universidad Nacional Autónoma de México. Mexico City, pp. 128, 129, 131.
- HERNÁNDEZ-X., E. 1993. Aspects of plant domestication in Mexico: a personal view. Pp. 733-753 in T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, (editors), *Biological Diversity of Mexico*. Oxford University Press, New York.
- HUGHES, C.E. 1993. *Leucaena* Genetic Resources: The OFI *Leucaena* Seed Collections and a Synopsis of Species Characteristics. Oxford Forestry Institute. Department of Plant Sciences. University of Oxford, Oxford.
- , 1998a. A second spontaneous hybrid in *Leucaena* Benth. (Leguminosae: Mimosoideae). *Pl. Syst. Evol.* 212:53-77.
- , 1998b. Monograph of *Leucaena* (Leguminosae-Mimosoideae). *Systematic Botany Monographs* 55:1-244.
- , and S. A. Harris. 1994. The characterisation and identification of a naturally occurring hybrid in *Leucaena* Benth. (Leguminosae: Mimosoideae). *Pl. Syst. Evol.* 192:177-197.
- JÄCKLEIN, K. 1974. Un Pueblo Popoloca. Colección SEPINI. Serie antropología social, no. 25. Instituto Nacional de Antropología e Historia, Mexico City.
- JONES, R.J. and MEGARRITY, R.G. 1986. Successful transfer of DHP-degrading bacteria from Hawaiian goats to Australian ruminants to overcome the toxicity of *Leucaena*. *Australian Veterinary Journal* 63(8):259-262.
- KELLY, I. and A. PALERM. 1952. *The Tajin Totonac*. Institute of Social Anthropology, Publication No. 13.
- KENNEDY, D. S. 1992. *Recetas rescatadas*, 5: Guajes. *México Desconocido* 14 (185):48-51.
- LAZOS, C., E. and M.E. ÁLVAREZ-BUYLLA R. 1988. Ethnobotany in a tropical-humid region: The home gardens of Balzapote, Veracruz, Mexico. *Journal of Ethnobiology*. 8 (1):45-79.

- MACNEISH, R. S., F.A. PATERSON and K.V. FLANNERY. 1970. *Ceramics. The Prehistory of the Tehuacán Valley*, vol. 3. University of Texas Press, Austin.
- MARTIN, G. J. 1995. *Ethnobotany: A Methods Manual*. Chapman and Hall, New York.
- MARTÍNEZ, M. 1979. *Catálogo de Nombres Vulgares y Científicos de Plantas Mexicanas*. Fondo de Cultura Económica, Mexico City.
- MEDELLÍN, M., S. 1990. Manejo agrosilvícola tradicional en una comunidad totonaca de la costa de Veracruz, México. Pp. 11-26 in Posey *et al.* (editors), *Ethnobiology: Implications and Applications*. Proceedings of the First International Congress of Ethnobiology. Belém, 1988. Vol.2.
- MESSER, E. 1978. Zapotec plant knowledge classification, uses and communication about plants in Mitla, Oaxaca, Mexico. In K. Flannery and R. Blanton (eds.). *Prehistory and Human Ecology of the Valley of Oaxaca*, Volume 5, Part 2. *Memoirs of the Museum of Anthropology*, No. 10. University of Michigan, Ann Arbor.
- PEREDES-COLÍN, J. 1977. *Apuntes Históricas de Tehuacán*. Third edition. B.-Costa-Amic, Mexico City.
- PARRA, H. 1983. *Especies nativas de utilidad alimenticia de Baja California Sur*. Segunda reunión nacional sobre ecología, manejo y domesticación de las plantas útiles del desierto. Pp. 53-68 in Special publication no. 43. Secretaría de Agricultura y Recursos Hidráulicos. Instituto Nacional de Investigaciones Forestales, Mexico City.
- RICO-GRAY, V., J. G. GARCÍA-FRANCO, A. CHEMAS, A. PUCH and P. SIMA, 1990. Species composition, similarity, and structure of Mayan homegardens in Tixpeul and Tixcacaltuyub, Yucatan, Mexico. *Economic Botany* 44(4):470-487.
- RZEDOWSKY, J. 1978. *La Vegetación de México*. Limusa, Mexico City.
- SESSÉ, M. and J. M. MOCIÑO. 1887. *Flora Mexicana*. First edition. Oficina Tipográfica de la Secretaría de Fomento, Mexico City. pp. 257.
- _____ and _____. 1893. *Plantae Novae Hispaniae*. Second edition. Oficina Tipográfica de la Secretaría de Fomento, Mexico City.
- SIMÉON, R. 1977. *Diccionario de la Lengua Nahuatl o Mexicana*. Siglo XXI. Mexico City.
- STANDLEY, P. 1922. *Trees and Shrubs of Mexico*. *Contributions of the United States National Herbarium* 23:366-369.
- _____ and S. CALDERÓN. 1925. *Lista Preliminar de Plantas de El Salvador*. El Salvador.
- VÁZQUEZ, R., M. C. 1986. *El uso de plantas silvestres y semicultivadas en la alimentación tradicional en dos comunidades campesinas del Sur de Puebla*. B. Sc. thesis. Facultad de Ciencias. Universidad Nacional Autónoma de México, Mexico City.
- VINES, R. A. 1960. *Trees, Shrubs and Woody Vines of the Southwest*. University of Texas Press, Austin.
- VOGT, G. 1991. *In vivo* decondensation of chromatin and nucleolar fibrillar component by *Leucaena leucocephala* ingredient. *Biol Cell* 72:211-215.
- ZÁRATE, S. 1984. Domesticación incipiente del "Guaje zacatzin." P p. 237-238 in *Resúmenes del 9º Congreso Mexicano de Botánica*, no. 381, Mexico City.
- _____. 1987. Taxonomic identity of *Leucaena leucocephala* (Lam.) de Wit, with a new combination. *Phytologia* 63 (4): 304-306.
- _____. 1994. Revisión del género *Leucaena* Benth. en México. *Anales del Instituto de Biología, Serie Botánica* 65 (2):83-162.
- _____. 1997. Domestication of cultivated *Leucaena* (Leguminosae) in México: The sixteenth century documents. *Economic Botany* 51(3):238-250.
- _____. 1998. La domesticación de *Leucaena* (Fabaceae Mimosoideae) en México. *Boletín de la Sociedad Botánica de México* 62:141-155.
- _____. 1999. *Estudios sistemáticos del proceso de domesticación del género Leucaena en México*. Doctoral thesis. Facultad de Ciencias, UNAM. Mexico City.
- ZIZUMBO, D. and P. COLUNGA. 1982. *Los Huaves: Apropiación de los Recursos Naturales*. Departamento de Sociología Rural-Universidad Autónoma de Chapingo, Chapingo.

APPENDIX 1.—Names, uses and distribution of *Leucaena* spp.

Taxon ¹	Common names ² / Language/Meaning	Location	Distribution	Uses	Management Status
<i>L. macrophylla</i> Benth. subsp. <i>macrophylla</i>	<i>guaje blanco</i> ^a / Spanish / "white guaje"	Morelos	Sierra Madre del Sur, from Nayarit to Oaxaca, Sierra Norte de Puebla	Dry seeds eaten toasted; tender leaves eaten raw	Wild
	<i>guajillo</i> ^b / Spanish / "small guaje"	Guerrero		Tender seeds eaten raw	Wild
	<i>Zacaguaje</i> ^b / Spanish (from Nahuatl <i>zacatl</i> <i>uaxin nduva cualli</i> ^c , and <i>nduva cuallo</i> ^d / Mixtec / "horse guaje"	Oaxaca		Tender seeds eaten raw	Wild
	<i>guaje de venado</i> ^a / Spanish / "deer's guaje"	Mexico		Tender seeds eaten raw; fresh pods sold in local markets ^e	Wild
<i>L. macrophylla</i> Benth. subsp. <i>nelsonii</i> (Britton et Rose) Zárata	<i>guaje de risa</i> ^a / Spanish / "laughter guaje"	Guerrero	Sierra Madre del Sur, from Guerrero to Chiapas; Veracruz	tender seeds eaten raw or cooked	Wild
<i>L. lanceolata</i> S. Watson subsp. <i>lanceolata</i>	<i>guajillo</i> ^f / Spanish / "small guaje"	Baja California Sur	Baja California Sur, Sierra Madre Occidental and Sierra Madre del Sur, from Chihuahua to Chiapas, Veracruz	Immature legumes eaten raw; dry seeds eaten toasted and ground to powder ^f	Wild
	<i>guajillo</i> ^g / Spanish / "small guaje"	Sinaloa, Michoacán, Guerrero		Tender seeds eaten raw	Wild
	<i>bolillo</i> ^g / Spanish / "small balls tree"	Sinaloa		Tender seeds eaten raw	Wild

APPENDIX 1.—Names, uses and distribution of *Leucaena* spp. (continued)

Taxon ¹	Common names ² / Language/Meaning	Location	Distribution	Uses	Management Status
	<i>nasiva</i> or <i>vasina</i> ^g / Guarigia/“guaje guaje”	Sonora Costa Grande, Guerrero		Forage	Favored in Pastures
	<i>napajteam</i> ^h / Huave/unknown	San Mateo del Mar, Oaxaca		Forage; living fence; wood for utensils	Cultivated in living fences
	<i>yaga-la-sha-xi</i> ^a / Coast Zapotec/ “rainy season guaje”	Tehuantepec Isthmus, Oaxaca		Tender seeds eaten raw	Planted along irrigation canals
	<i>angelito</i> ^a /Spanish/ “little angel”	Tehuantepec Isthmus, Oaxaca		Quality firewood	Wild
	<i>guaje sabanero</i> ^a / Spanish/ “savanna guaje”;	Pochulta, Oaxaca		Tender leaves and seeds eaten raw; medicinal for infections	Wild
	<i>ejote</i> ^a /Spanish/ “string bean guaje”				
	<i>guaje de zopilote</i> ^a / Spanish/ “vulture guaje”	Llano Grande, Oaxaca		Tender seeds and leaves eaten raw	Wild
	<i>da yuuh</i> ^a /Chatino/ “wild guaje”				
<i>L. lanceolata</i> S. Watson subsp. <i>sousae</i> Zárate	<i>guaje</i> ; <i>ejote</i> ^a /Spanish/ “string-bean tree”	Pochulta, Oaxaca	Southern Pacific Coast from Michoacán to Chiapas	Tender leaves and seeds eaten, taste sweeter, less pungent than that of subsp. <i>lanceolata</i>)	Wild
<i>L. retusa</i> Benth ex A. Gray	golden-ball lead tree ⁱ / English	Texas and New Mexico	Texas, New Mexico, Coahuila, Chihuahua	Browsed by cattle	Wild

<i>L. shannonii</i> J.D. Smith subsp. <i>shannonii</i>	<i>cascahuite</i> ^j /Spanish, from Nahuatl <i>uaxcuahuitl</i> / "guaje tree"	El Salvador	Chiapas to Nicaragua	Unknown	Wild
	<i>guaje</i> ^{a,j}	Chiapas, Guatemala, Honduras, El Salvador, Nicaragua		Living Fence	Wild and cultivated in living fences
	<i>frijolillo</i> ⁱ /Spanish/ "small bean"	Honduras		Unknown	Wild
	<i>guajillo</i> ⁱ /Spanish/ "small guaje"	Guatemala		Unknown	Wild
	<i>vainá</i> ⁱ /Spanish/ "legume"	Nicaragua		Unknown	Wild
<i>L. shannonii</i> J.D. Smith subsp. <i>salvadorensis</i> (Standley <i>ex</i> Britton <i>et</i> Rose) Zárate	<i>guacamaya de montaña</i> ^k / Spanish/ "mountain guacamaya"	Joroco, Morazán, El Salvador, Estelí, Nicaragua	El Salvador, Honduras, and Guatemala	Unknown	Wild
	<i>sepia</i> ^l /Spanish/ probably refers to dye or color <i>guaje</i> ^j				
<i>L. shannonii</i> J.D. Smith subsp. <i>magnifica</i> Hughes	<i>guaje</i> ^l ; <i>vainillo</i> ^l /Spanish/ "small legume tree"	El Rincón, Guatemala	Chiquimula Valley, Guatemala	Unknown	Favored

APPENDIX 1.–Names, uses and distribution of *Leucaena* spp. (continued)

Taxon ¹	Common names ² / Language/Meaning	Location	Distribution	Uses	Management Status
<i>L. leucocephala</i> (Lam.) de Wit subsp. <i>leucocephala</i>	<i>huaxi, uaxim, xaxim</i> ^{b,n} / probably derived from Nahuatl/“guaje”	Yucatán	Gulf of Mexico, Yucatán Peninsula and Tehuantepec Isthmus	Medicinal, antiparasitic and used against chicken lice; not eaten	Favored in milpas and intensively managed pastures
<i>L. leucocephala</i> (Lam.) de Wit subsp. <i>glabrata</i> (Rose) Zárate	<i>guaje verde</i> ^{a,c,d} /Spanish/ “green guaje”	Morelos, Guerrero	Widespread in lowlands, Central and South Mexico to Nicaragua	Tender seeds eaten raw or cooked; leaves eaten raw; medicinal; sold in markets	Cultivated and probably escaped in disturbed habitats, or native in riparian habitats
	<i>lelekes</i> or <i>li.l_k</i> <i>kiwililiak liliake</i> ^{a,m} / Totonac/ “smelly legume”	Papantla, Veracruz		“	Favored and planted in slash and burn milpas
	<i>guash</i> ^a /Nahuatl/ guaje	Northern Puebla		“	“
	<i>guaje blanco</i> ^a /Spanish/ “white guaje”	Oaxaca		“	Cultivated
	<i>auaxin</i> ^{a,o} /Nahuatl/ “water guaje”	Guerrero		“	Cultivated, escaped or native in riparian habitats
	<i>calluaxin</i> ^a /Nahuatl/ “horse guaje”				

	<i>nduva cui</i> ^{a,c,d} / Mixtec / "green guaje" <i>manso</i> ^c / Spanish / "tame guaje"				
<i>L. esculenta</i> (Moc. Et Sessé ex A. DC.) Benth. subsp. <i>esculenta</i>	<i>guaje rojo</i> ; <i>guaje</i> <i>colorado</i> ^{a,i} / Spanish / "red guaje"	Jalisco, Michoacán, Guerrero, Puebla, Oaxaca	Sierra Madre del Sur, Jalisco, Hidalgo, Puebla, Veracruz, Michoacán, México, Morelos, Guerrero, Oaxaca		
	<i>uaxin</i> ^{a,o} / Nahuatl / <i>guaje</i>	Guerrero, Morelos, Puebla		Seeds and leaves eaten raw; tender seeds cooked; dry seeds eaten toasted; sold in markets	Wild, planted, favored, escaped
	<i>uaxin chichiltic</i> ^a / Nahuatl / "red guaje"				
	<i>hueyuaxin</i> ^{a,o} / Nahuatl / "large guaje" <i>guaje de Castilla</i> ^a / Spanish / "Castilian guaje"				
	<i>Iya kures</i> ^{a,p} / Mitla Zapotec / "dry season guaje"	Oaxaca			Planted, favored, ruderal
	<i>nduva cuaá</i> ^{a,c,d} / Mixtec / "red guaje"	Guerrero, Puebla, Oaxaca			planted, favored, wild
	<i>nduva cuaá nanu</i> ^c / Mixtec / "wide red guaje"	Guerrero			

APPENDIX 1.—Names, uses and distribution of *Leucaena* spp. (continued)

Taxon ¹	Common names ² / Language/Meaning	Location	Distribution	Uses	Management Status
	<i>nduva cuaá cuali</i> ^c / Mixtec / "thin red guaje"				
	<i>libad lo</i> ^a / Coast Mixtec / "red guaje"	Oaxaca			Planted, favored
	<i>al pa la</i> ^b / Chontal/ unknown				
	<i>pa la</i> ^b / Chontal/ unknown				
	<i>yaga la</i> ^{a,b} / Zapotec / "guaje"				
	<i>éfé</i> ^a / Otomi / "guaje"	Hidalgo			
<i>L. esculenta</i> (Moc. et Sessé ex A. DC.) Benth. subsp. <i>paniculata</i> (Britton et Rose) Zárate	<i>guaje barbero</i> ^a / Spanish / "barbers guaje"	Morelos	Zacatecas, Puebla, Morelos, Oaxaca	Believed to cause hair to fall when eaten	Wild
	<i>pepetoaxin</i> ^o / Nahuatl / "mucilaginous guaje"				
	<i>guajal de campo</i> ^a / Spanish / "wild guaje"	Oaxaca		Tender seeds occasionally eaten	Wild
	<i>lobada le eg</i> ^a / Zapotec / "wild guaje"				
	<i>Iya gusgih</i> ^{a,p} / Zapotec / "rainy-season guaje"				
	<i>guajal de cerro</i> ^a / Spanish / "wild guaje tree"				

	<i>guaje colorado</i> ^a /Spanish/ "red <i>guaje</i> "	Puebla		Tender seeds eaten; sold in markets	Favoured and planted
	<i>nduva nduchi</i> ^{c,d} /Mixtec/ "bean <i>guaje</i> "	Guerrero		"	Wild
	<i>guaje de guanduchi</i> ^c / Spanish/"bean <i>guaje</i> "				
<i>L. esculenta</i> (Moc. et Sessé ex A. DC.) Benth. subsp. <i>matudae</i> Zárate	<i>guaje retinto</i> ^a /Spanish/ "dark red <i>guaje</i> "	Guerrero	Central Balsas Basin	seldom eaten; bark vulnerable and in magic medicine	Wild
	<i>chiquimoluaxin</i> ^a / Nahuatl/ "nightingale <i>guaje</i> " or "cleft-wood <i>guaje</i> "				
	<i>guaje jilguero</i> ^j /Spanish/ "nightingale <i>guaje</i> "				
	<i>guaje chismoso</i> ^a / Spanish/"gossip <i>guaje</i> "				
	<i>guaje brujo</i> ^{a,j} /Spanish/ "witch <i>guaje</i> "				
	<i>nduva ticuandá</i> ^a / Mixtec/unknown				
	<i>guaje ticuanda</i> ; <i>guaje de hielote</i> ^a / Spanish/unknown				
<i>L. collinsii</i> Britton et Rose subsp. <i>collinsii</i>	<i>guaje</i> ; <i>guaje colorado</i> ^a / Spanish/"red <i>guaje</i> "	Chiapas	Chiapas to Northern Guatemala	Tender seeds eaten raw	Wild and planted in living fences
	<i>guash</i> ^{a,j} /Nahuatl/ "guaje"				
	<i>guash de monte</i> ^j / Nahuatl and Spanish/ "wild <i>guaje</i> "				

APPENDIX 1.—Names, uses and distribution of *Leucaena* spp. (continued)

Taxon ¹	Common names ² / Language/Meaning	Location	Distribution	Uses	Management Status
	<i>chijlip</i> ¹ /Tojolabal/ "sweet guaje"				
<i>L. cuspidata</i> Standley subsp. <i>cuspidata</i> and <i>L. cuspidata</i> Standley subsp. <i>jacalensis</i> Zárate	' <i>éfé</i> ^a /Otomi/"guaje" ' <i>éfé de cerro</i> ¹ /Spanish/ "wild guaje" <i>uaxi</i> ^a /Nahuatl/"guaje"	Hidalgo	San Luis Potosi, Hidalgo, Queretaro	Tender seeds eaten raw; sold in markets	Wild, cultivated
<i>L. confertiflora</i> Zárate subsp. <i>confertiflora</i>	<i>guaje</i> ^a /Spanish/"guaje"	Oaxaca, Puebla	Oaxaca, Puebla	Unknown	Wild
<i>L. confertiflora</i> Zárate subsp. <i>adenotheloidea</i> Zárate	<i>guaje zacatzin</i> ^a / from Nahuatl/ "wild guaje"	Puebla	Sierra de Zongolica, Puebla	Tender seeds eaten raw or cooked; sold in markets	Wild, planted
<i>L. diversifolia</i> (Schldl.) Benth. subsp. <i>diversifolia</i>	<i>guaje</i> ; <i>guaje blanco</i> ^a / Spanish/"white guaje"	Jalapa, Veracruz	Central Veracruz	Tender seeds eaten raw	Wild, tolerated
<i>L. diversifolia</i> (Schldl.) Benth. subsp. <i>stenocarpa</i> (Urban) Zárate	<i>La-aye-ti</i> ^a /Zapotec/ "small guaje" <i>lobadaviyin</i> ^a / Zapotec/"bird guaje" <i>shashib</i> ; <i>shashibtez</i> ; <i>xaxib</i> ; <i>ch'ich'n̄</i> ¹ / Tzeltal/unknown	Oaxaca	Sinaloa, Durango, Jalisco, México, Morelos, Guerrero, Oaxaca, Chiapas, Guatemala, Honduras, El Salvador	Tender seeds eaten raw "	Wild "

<i>L. pulverulenta</i> (Schldl.) Benth.	<i>guañas</i> ^a /Chichimec/ "guaje"	San Luis Potosí	Eastern flank of the Sierra Madre Oriental, Nuevo León, Tamaulipas, San Luis Potosí, Hidalgo, Veracruz, Oaxaca	Tender flower buds and seeds eaten raw	Wild
	<i>guaje; guashe; huaché</i> / from Nahuatl/"guaje"	Puebla and Hidalgo (Sierra Norte de Puebla)		"	"
	<i>lilakiwi</i> ^{a,m} /Totonac/ "guaje tree"	Totonacapan in Veracruz		"	"
	<i>tze</i> ^a /Mazatec/"guaje"	Oaxaca, Sierra de Hautla		"	"
	<i>thuk</i> ^r /Huastec/"guaje"	San Luis Potosí		Tender leaves and seeds eaten raw; leaves in medicinal preparations	
<i>L. X brachycarpa</i> (Urban) Zárate	Unknown	Oaxaca, Eastern Sierra Mazateca		Unknown	Wild
<i>L. greggii</i> S. Watson	Unknown	Coahuila, Nuevo León		Unknown	Wild
<i>L. involucrata</i> Zárate	<i>barra blanca</i> ⁱ /Spanish/ "white bar"	Sonora	Sonora	Unknown	Wild

¹Taxa follow Zárate (1994). Central American taxa are included for completeness.

²Sources: a. Field observation; b. Martínez 1979; c. Casas and Caballero 1996; d. Casas *et al.* 1994; e. R. Bye and E. Linares, personal communication; f. Parra 1983; g. González-Ortega 1929; h. Zizumbo and Colunga 1980; i. Vines 1960; j. Herbarium label; k. Standley and Calderón 1925; l. Hughes 1993; m. Kelly and Palerm 1952; n. Barrera *et al.* 1980; o. Hernández 1960; p. Messer 1978; q. Casas 1992; r. Alcorn 1984.