Traditional Management and Morphological Variation in *Leucaena esculenta* (Fabaceae: Mimosoideae) in the Mixtec Region of Guerrero, Mexico[1]

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Casas, Alejandro *(Jardín Botánico, Instituto de Biología, U.N.A.M. Apartado Postal 70-614, México, D.F. 04510, México. The University of Reading. Department of Agricultural Botany, School of Plant Sciences, Whiteknights PO Box 221, Reading RG6 6AS, UK) and* **Javier Caballero** *(Jardín Botánico, Instituto de Biología, U.N.A.M. Apartado Postal 70-614, México, D.F. 04510, México).* TRADITIONAL MANAGEMENT AND MORPHOLOGICAL VARIATION IN *LEUCAENA ESCULENTA* (FABACEAE: MIMOSOIDEAE) IN THE MIXTEC REGION OF GUERRERO, MEXICO. *Economic Botany 50(2):167–181, 1996.*
Ethnobotanical information about uses, management and traditional classification of Leucaena esculenta *by the Mixtec in Guerrero, Mexico, is presented. This plant is mainly used as human food. Buds of leaves and flowers as well as seeds and young pods are the main edible parts. Size, flavor and digestibility of seeds and pods are shown to be important in the Mixtec classification of* Leucaena *species and in selection of trees to harvest during gathering. Artificial selection in* L. esculenta *subsp.* esculenta *by the Mixtec occurs not only under cultivation, but also in wild populations where people eliminate some individuals while promoting the growth of others with favorable phenotypes. Morphological characters of seeds and pods of individual trees of this subspecies were measured in order to compare phenotypic variation in populations subject to different regimes of management. Samples of trees were analyzed from a) a wild population not affected by intentional disturbances; b) a wild population selectively managed* in situ; *and c) a sample of cultivated individuals. Ordination methods and analysis of variance were used to examine differences between populations. A marked divergence between the three samples was found, especially between the wild populations managed and unmanaged. The frequency of the phenotypes preferred by people was found to be higher in the wild population* in situ *managed. Our study confirms that through* in situ *forms of management, people are able to modify the phenotypic structure of plant populations. Possible routes of plant domestication within plant populations* in situ *are suggested.*

Manejo Tradicional y Variacion Morfologica en *Leucaena esculenta* (Fabaceae, Mimosoideae) en la Region Mixteca de Guerrero, México. *Se presenta información etnobotánica sobre usos, manejo y clasificación tradicional de* L. esculenta *por los Mixtecos de Guerrero, México. Esta planta es usada principalmente como alimento humano. Los brotes de hojas y flores, asi como las semillas y vainas inmaduras son las principales partes comestibles. El tamaño, el sabor y la digestibilidad de las semillas y vainas son caracteres importantes en la clasificación Mixteca de las especies de* Leucaena, *asi como en la elección de árboles a cosechar durante la recolección. Los Mixtecos efectúan selección artificial en* L. esculenta *subsp.* esculenta *durante su cultivo, pero también en poblaciones silvestres, donde los campesinos eliminan algunos individuos y mantienen en pie otros con fenotipos favorables. Se midieron caracteres morfológicos de semillas y vainas de árboles de esta subespecie con el fin de comparar variabilidad fenotípica en poblaciones sometidas a diferentes formas de manejo. Se analizaron muestras colectadas en árboles de una población silvestre sin aparente perturbación intencional, de una población silvestre cuyos individuos fueron dejados en pie selectivamente* in situ *y de una muestra de individuos cultivados. Se utilizaron métodos de ordenación y análisis de varianza para examinar diferencias entre las muestras. Se encontró una marcada divergencia entre las muestras, destacando la divergencia entre las poblaciones silvestres que son manejadas en forma diferente. La frecuencia de los fenotipos preferidos por la gente fue mayor en la población manejada* in situ. *Esto mostró que a través de formas de manejo de plantas* in situ, *la gente es capaz de modificar la estructura fenotípica de las poblaciones vegetales. Se sugieren posibles rutas de domesticación en poblaciones de plantas* in situ.

Key Words: domestication; ethnobotany; *Leucaena esculenta*; Mixtec Indians; Mexico.

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Leucaena Benth. is a plant genus of a promising economic value, used mainly as human food, fodder, wood and for soil conservation. This genus is native to the New World, and it is distributed from southwestern United States through middle South America (Zárate 1982, 1984, 1994). *L. leucocephala* (Lam.) de Wit is the most widely known and utilized species of the genus. Nevertheless, the other species [15 according to Hughes (1993) as well as Sorensson and Brewbaker (1994) and 14 according to Zárate (1994)] are also important plant resources as suggested by the fact that all of them have been commonly used for food by indigenous people in Mexico over a long time. Smith (1986) reported the presence of remains of *L. esculenta* (Moc. et Sessé ex A.DC.) Benth. seeds and pods in strata approximately 10 000 years old, from archaeological excavation of caves at Guilá Naquitz, Oaxaca, Mexico. Although the taxonomic identity of these remains has been questioned by Zárate (1994), in the Tehuacán Valley, Smith (1967) and MacNeish (1967) certainly found the presence of *L. esculenta* seeds and pods in strata of about 8000 years old. However, it is important to mention that these dates have more recently been subject to revision (Long et al. 1989).

Five taxa have been reported to be cultivated in Mexico: *L. lanceolata* S. Watson, *L. confertiflora* Zárate subsp. *adenotheloidea* Zárate (Zárate 1994), *L. esculenta* subsp. *paniculata* (Britton and Rose) Zárate (Zárate 1994), *L. esculenta* subsp. *esculenta, L. leucocephala* subsp. *leucocephala,* and *L. leucocephala* subsp. *glabrata* Zárate (Zárate 1987). Some of these species are traditionally cultivated by a number of Indian groups, mainly in home gardens. For example, *L. lanceolata* was reported to be grown by the Huave of San Mateo del Mar, Oaxaca (Zizumbo and Colunga 1982), while *L. confertiflora* subsp. *adenotheloidea* is cultivated by the people of San Pedro Chapulco, Puebla (Zárate 1994). *L. esculenta* subsp. *paniculata* is cultivated in San Pedro Chapulco and in other areas of central Mexico as well (Zárate 1994). *L. leucocephala* subsp. *glabrata,* since ancient times grown in home gardens in some parts of Mexico has recently been introduced into extensive cultivation, mainly for fodder in tropical lowlands. *L. esculenta* subsp. *esculenta* has been reported as an important native crop in most of Central Mexico (Casas 1992), and is, along with *L. leucocephala* subsp. *glabrata,* by far the most widely cultivated species of *Leucaena* in Mexico.

L. esculenta subsp. *esculenta,* is commonly known as the "guaje rojo" (red guaje). It has a wide distribution as a cultivated plant. It has been reported from the States of Jalisco, Hidalgo, Veracruz, Michoacán, México, Puebla, Morelos, Oaxaca, Guerrero, Zacatecas, Colima, Nayarit and Chiapas (Casas 1992; Hughes 1993; Zárate 1982). Wild populations of this species have been found only in the Balsas River basin, mainly in La Montaña region of the State of Guerrero (Casas 1992).

La Montaña de Guerrero is one of the most important indigenous regions of Mexico, with almost 75% of its population belonging to the Nahua, Mixtec, Tlapanec and Amuzgo groups (Casas, Viveros, and Caballero 1994). In this region, subsistence is based on the traditional cultivation of corn, beans and squashes, complemented by goat and cattle raising (Casas et al. 1987). Gathering is also an important activity for subsistence. Viveros, Casas, and Caballero (1993) found that edible adventives constitute approximately 10% of the total annual food consumption among the Mixtec of this region. Casas, Viveros, and Caballero (1994) estimate that there are nearly 150 species of edible adventives and wild plants in La Montaña de Guerrero. Among them, three species of *Leucaena,* locally called "guajes," play an important role in the campesino diet.

In this region, pods, seeds and young leaves of *L. esculenta* subsp. *paniculata* and *L. macrophylla* Benth. are gathered only from wild populations. These populations are part of the tropical deciduous forest at altitudes between 800 and 1480 m. a.s.l. *L. leucocephala* is found only in cultivation, having been introduced to the region by government sponsored reforestation projects. During these projects, it failed to establish in the forests and only survived in homegardens. Wild populations of *L. esculenta* subsp. *esculenta* also occur in the tropical deciduous forest. This species is also found as a weedy or ruderal plant in disturbed areas with secondary vegetation. It is also cultivated in homegardens and other agricultural contexts. Human interactions with this plant include the harvest of wild trees in the forests, the retention

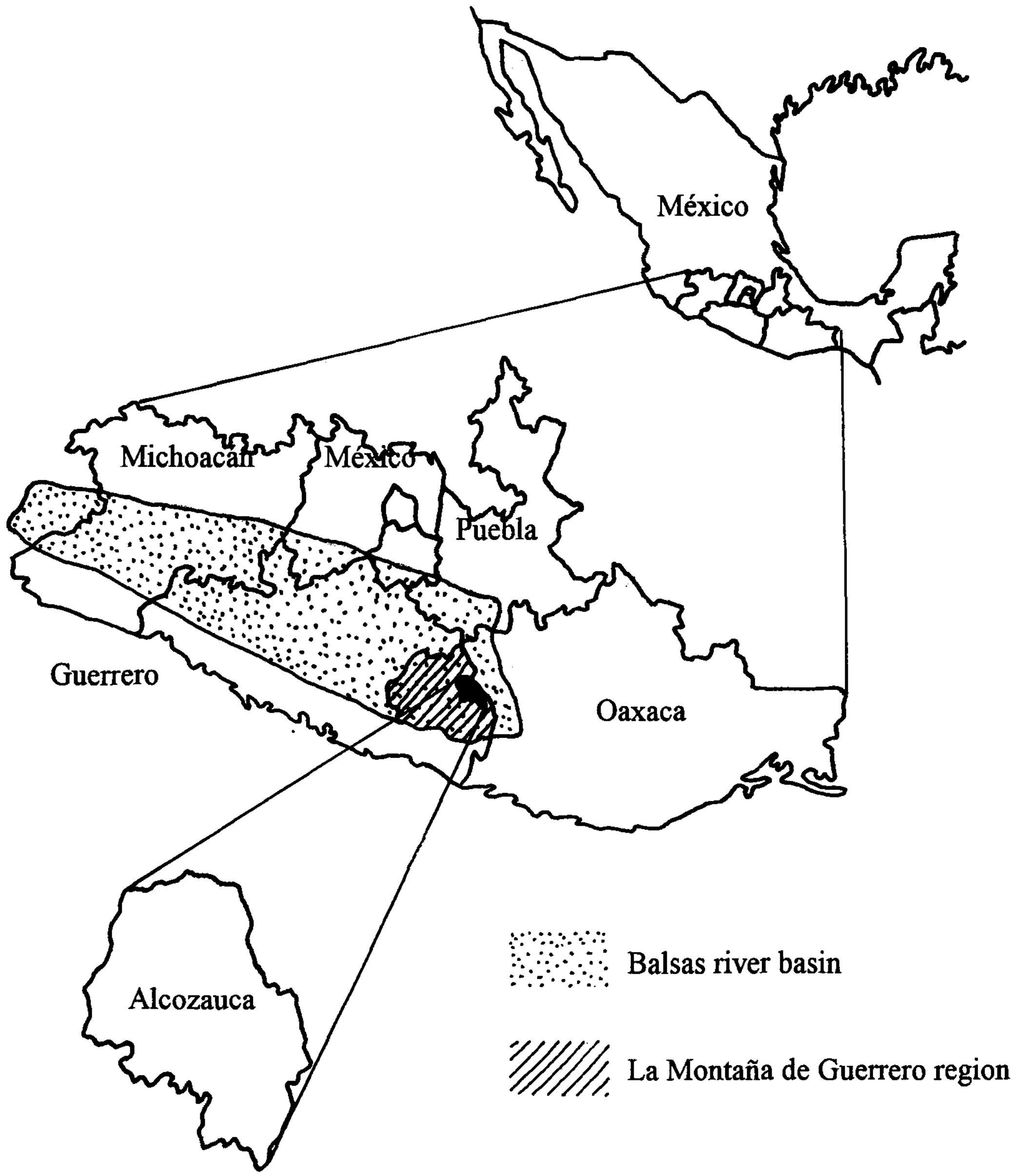

Fig. 1. Study area.

or tolerance of trees in crop lands, as well as the cultivation of trees in home gardens. An aparent variation in morphological characteristics of both seeds and pods is observed between wild, tolerated and cultivated trees. This variation suggests that the "red guaje" might be undergoing a process of domestication by the local people. Moreover, the coexistence of both wild and cultivated populations, the wide morphological variation as well as the occurrence of the different interactions mentioned above, may indicate that the Balsas River basin is at present, a center of domestication of *L. esculenta* subsp. *esculenta*, and that cultivated forms of this species are probably being introduced to other parts of Mexico.

This paper describes the forms of use and management as well as traditional classification of *L. esculenta* subsp. *esculenta* by the Mixtec, and analyzes the patterns of morphological vari-

TABLE 1. PROVENANCE DATA FOR WILD INDIVIDUALS (W).

Individuals	Collecting number	Altitude (m.a.s.l.)	Habitat	Tree form	Height (m)	Signs of gathering
W1	605	1430	TDF	Shrub	3	NO
W2	607	1440	TDF	Shrub	3	NO
W3	610	1400	TDF	Tree	4	YES
W4	612	1400	TDF	Shrub	3	YES
W5	615	1375	TDF	Shrub	3	YES
W6	617	1370	TDF	Tree	5	NO
W7	623	1370	TDF	Tree	6	NO
W8	625	1350	TDF	Shrub	2	NO
W9	628	1330	TDF	Shrub	3	NO
W10	606	1425	TDF	Shrub	4	YES
W11	608	1435	TDF	Tree	8	NO
W12	609	1400	TDF	Tree	4	YES
W13	611	1400	TDF	Tree	5	YES
W14	613	1380	TDF	Shrub	3	NO
W15	614	1375	TDF	Shrub	3	NO
W16	618	1360	R	Tree	6	YES
W17	619	1360	R	Tree	7	NO
W18	620	1360	R	Shrub	6	NO
W19	621	1360	R	Tree	6	NO
W20	622	1360	R	Tree	8	YES

TDF = Tropical Deciduous Forest. R = Roadsides.

ation in pods in relation to management. Based on this evidence, the importance of in situ management in the process of domestication of *L. esculenta* subsp. *esculenta* is discussed.

METHODS

A survey of *L. esculenta* subsp. *esculenta* was conducted in the States of Morelos, Puebla, Oaxaca and Guerrero, within the Balsas River basin, where wild populations and cultivation of this species occur. The survey was conducted with a greater detail in "La Montaña" region in northeast Guerrero (Fig. 1). This survey included the collection of dried specimens as well as the recording of ethnobotanical information on use and management of *L. esculenta* subsp. *esculenta*. The specimens collected were deposited in the National Herbarium of Mexico (MEXU) under Viveros, J. L. and A. Casas collection numbers. Field trips and visits to traditional indigenous markets were made to observe and record the diversity of form, size, flavor and other attributes of seeds and pods of *L. esculenta* in use, management methods, and traditional nomenclature and classification in different cultural and environmental situations. A total of 28 Mixtec, Nahua, and Mestizo people participated as consultants. They provided ethnobotanical information through open ended interviews; detailed information on management was obtained by indepth interviews. The Mixtec folk classification of "guajes" was elicited with both structured and open interviewing. Structured interviewing consisted in presenting dried specimens of different species of *Leucaena* and infraspecific variants to a sample of five informants, and asking for the corresponding plant name.

Two populations and one sample of cultivated individuals of *L. esculenta* subsp. *esculenta* from the municipality of Alcozauca at La Montaña region were sampled for studying patterns of morphological variation in pods. The two populations represented different forms of management of guaje trees by the Mixtec Indians. The first is a wild population which has not been subjected to intentional clearings for at least the last fifty years. This population is located 25 km west of Alcozauca in a well preserved forested area of tropical deciduous forest, which is traversed by a narrow footpath. Density of this population is 15 guaje trees per hectare. Altitude in this area ranges from 1300 to 1650 m. a.s.l., with a southeast aspect and thin soils derived from calcareous rocks. In this area, habit of *L. esculenta* subsp. *esculenta* varies from trees with a main stem, to shrubs branching near the base (Table 1). Sampled area was 1.6 ha. The second population is also wild but consists of individuals which have been selectively spared after many cycles of forest clearance involved in shifting cultivation of maize. This form of plant management corresponds to that defined as "tolerance" by Bye (1993), Caballero (1994) and Casas, Viveros, and Caballero (1994). Density of this population is 0.8 individuals per hectare. It is located on slopes west of Alcozauca between 1250 and 1700 m. Slopes have a southeast aspect, with deeper soils derived from volcanic rocks. This area forms part of the main zone of seasonal agriculture of Alcozauca. Prehispanic archaeological remains suggest that this area has been used for agriculture for over five centuries (Casas, Viveros, and Caballero 1994). The former tropical deciduous forest cover in this zone has been reduced to a number of patches of secondary vegetation in different successional stages (Table 2). This population is the most important source of food products of *L. esculenta*

TABLE 2. PROVENANCE DATA FOR TOLERATED INDIVIDUALS (T).

Individuals	Collecting number	Altitude (m.a.s.l.)	Habitat	Tree form	Height (m)	Signs of gathering
T1	597	1580	TDF	Tree	10	YES
T2	599	1580	TDF	Tree	6	NO
T3	603	1590	OF	Tree	12	YES
T4	630	1530	ACF	Tree	4	YES
T5	635	1460	R	Tree	8	YES
T6	638	1450	CF	Tree	8	YES
T7	640	1450	CF	Tree	8	YES
T8	643	1420	ACF	Tree	8	YES
T9	647	1400	ACF	Tree	8	YES
T10	632	1530	ACF	Tree	5	YES
T11	595	1590	ACF	Tree	8	YES
T12	596	1580	ACF	Tree	7	YES
T13	634	1500	ACF	Tree	9	YES
T14	642	1420	CF	Tree	7	YES
T15	631	1525	ACF	Tree	5	YES
T16	633	1520	ACF	Tree	6	YES
T17	636	1450	R	Tree	9	YES
T18	639	1440	R	Tree	9	YES
T19	641	1430	ACF	Tree	12	YES
T20	644	1420	CF	Tree	5	YES

TDF = Tropical Deciduous Forest. ACF = Abandoned Corn Field. OF = Oak Forest. R = Roadside. CF = Corn Field.

subsp. *esculenta* for people of Alcozauca. Sampled area was 35 ha.

The third sample is formed by trees of *L. esculenta* subsp. *esculenta* cultivated in the homegardens in the town of Alcozauca. These home gardens are located at 1300 m. a.s.l. on deep alluvial soils (Table 3). Guaje trees are cultivated either from seeds collected in local wild populations, or from seeds of cultivated trees reported as native by local people. However, seeds from one individual tree of the sample were reported as introduced from the state of Morelos.

TABLE 4. MORPHOLOGICAL CHARACTERS ANALYZED.

Number	Character
1	Maximum seed length
2	Maximum seed width
3	Maximum seed thickness
4	Seed chamber length
5	Seed chamber width
6	Septum thickness
9	Maximum pod thickness
10	Pod peduncle length
11	Pod margin width
12	Number of ovules per pod
13	Number of seeds per pod
14	Number of aborted seeds per pod
15	Number of predated seeds per pod

Pod and seed samples were collected from a total of 48 trees, including twenty individuals from the wild population, twenty from the second population and eight from the trees cultivated in home gardens. Trees from wild and tolerated populations were collected along a transect of 100 m width across the altitudinal range over which *L. esculenta* subsp. *esculenta* is distributed. Cultivated individuals were collected from a random sample of home gardens. A total of 10 pods per tree were sampled. Both the pods and their seeds (n = 7600) were measured.

Fifteen quantitative characters of seeds and pods (Table 4) were measured. Characters 1, 2 and 3 are related to seed dimension. Dimensions of the seed chambers (variables 4, 5 and 6) are related to both seed and pod size. Variables 7, 8 and 9 account for pod size, and variable 10 is related to them. According to the Mixtec, pod margin width (variable 11) is related to the ease with which pods can be

TABLE 3. GENERAL INFORMATION ABOUT CULTIVATED INDIVIDUALS (C).

Individuals	Collecting number	Altitude (m.a.s.l.)	Parents	Common names	Height (m)	Age (years)
C1	570	1300	Cultivated (I)*	Zapoteco	10	15
C2	571	1300	Wild (N)**	Montañero	7	8
C3	582	1300	Cultivated (N)	Manso	8	10
C4	583	1300	Cultivated (N)	Manso	8	10
C5	648	1300	Wild (N)	Colorado	7	5
C6	649	1300	Wild (N)	Colorado	10	8
C7	650	1300	Wild (N)	Colorado	12	10
C8	651	1300	Wild (N)	Colorado	10	8

* I = Introduced. ** N = Native.

opened to obtain seeds when they are still immature. Variables 12, 13 and 14 refer to the number of seeds available as an edible resource. The number of seeds damaged by predators assesses the differential vulnerability of individuals to bruchid attack.

A basic data matrix of 15 characters for each of the 48 trees was constructed. State characters were the mean values for the respective character per tree. The basic data matrix was standardized using the linear transformation: $\mathbf{y}' = (\mathbf{y} - \mathbf{a})/\mathbf{b}$ where $\mathbf{y}'$ is the standardized value, **y** the variable mean value, **a** the average of values for this variable in all individuals, and **b** their standard deviation.

A correlation matrix between characters was calculated using the Pearson correlation coefficient (Sneath and Sokal 1973). A principal component analysis (PCA) was performed on this matrix using the Numerical Taxonomy and Multivariate Analysis System [NTSYS-PC version 1.8 (Rohlf 1993)]. The significance of the groupings shown by PCA was tested by means of a discriminant function analysis, (DFA) using the "Statistical Graphics System" (STATGRAPHICS), version 5.0.

A one-way analysis of variance was performed using those characters which showed to be important from PCA and which are related to both pod and seed size. For this, size of pods and seeds was estimated from the product of their length and width.

Results

Nomenclature and Classification

Folk nomenclature of *Leucaena* spp. follows the general principles of folk taxonomies proposed by Berlin, Breedlove, and Raven (1974) and Berlin (1992) and indicates the high cultural importance of these plants for indigenous people. In Spanish, as well as in some Indian languages such as Nahuatl and Mixtec, the species of *Leucaena* are grouped together into a generic taxon labelled by a primary lexeme. This taxon usually includes one or more specific taxa labelled by a secondary lexeme. In Spanish, the lexeme for all the species of *Leucaena* is "**guaje.**" This lexeme is derived from its equivalent in Nahuatl "**uaxi.**" In Mixtec, this generic taxon is labelled by the lexeme "**nduva.**" In this language, the generic taxon "**nduva**" is divided into four specific taxa which correspond to the scientific species and subspecies of *Leucaena* present in La Montaña of Guerrero. As it is shown in Fig. 2, in Mixtec, *L. esculenta* subsp. *esculenta* is labelled by the lexeme "**nduva cuaá,**" which means "red pod." This taxon includes two varietal taxa according to the shape and the size of the pods. Thus, the varietal taxon "**nduva cuaá cuali**" includes trees with small and thin pods, while the taxon "**nduva cuaá na/\nu**" includes trees with large and wide pods. The classification of red guaje at the varietal level based on morphological characters is

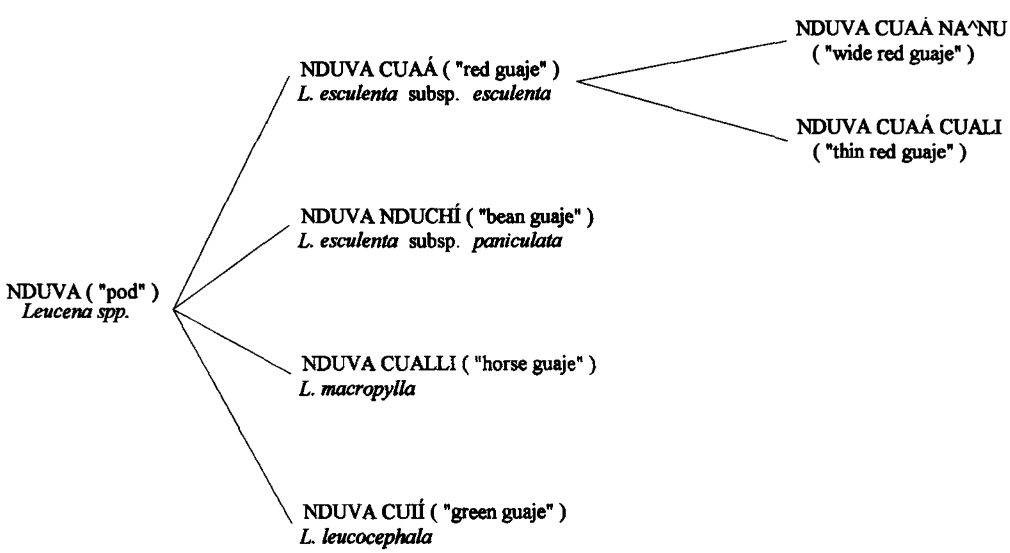

Fig. 2. Mixtec classification of *Leucaena* spp.

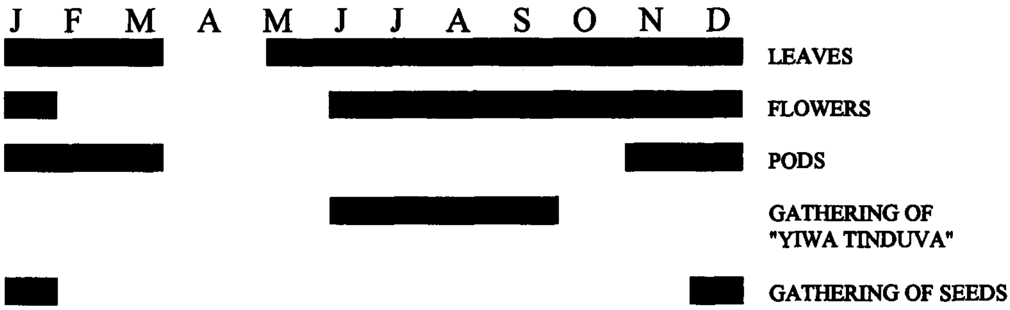

Fig. 3. Phenology of *Leucaena esculenta* subsp. *esculenta* in Alcozauca, Gro., and harvesting seasons of edible parts.

comparable with another classification based on utilitarian criteria. Thus, the Mixtec recognize three different varieties of *L. esculenta* subsp. *esculenta* according to their quality as edible resources:

A) "**Guaje manso o dulce**" ("sweet guaje"), known in Mixtec as "**nduva cuaá bishí**" ("**bishí**" means sweet). Seeds and pods of these plants have no bitter flavor, they are bigger than those of other varieties, and their immature fruits can be easily opened. Sweet guajes do not cause digestive disorders.

B) "**Guaje amargo**" ("bitter guaje"), or "**nduva cuaá yahtú**" (in Mixtec "**yahtú**" means bitter). Seeds of this kind of guaje have a bitter flavour and the pods are smaller and more difficult to open than "sweet guajes". Although "bitter guaje" may cause digestive disorders such as diarrhea, flatulence or stomach ache, their seeds may be eaten if roasted.

C) "**Guaje de vasca**" ("vomitory guaje"), or "**nduva cuaá ná**" in Mixtec. These guajes are bitter and contain toxic compounds which cause vomit when eaten.

It is important to mention that the lexeme "**nduva**" is also the Mixtec term for pod, and that other parts of the *Leucaena* trees are referred as parts of "**nduva**." For example, flowers are called "**ihta nduva**," roots "**tioo nduva**" and leaves "**iku nduva**." This indicates the cognitive and cultural significance of the pods for the Mixtec.

TABLE 5. EIGENVALUES.

Principal component	Eigenvalues	Percentage	% Accumulated
1	7.4678	49.79	49.79
2	2.1497	14.33	64.12
3	1.5186	10.12	74.24

USES

The main use of *L. esculenta* subsp. *esculenta* among the Mixtec is as human food. The immature pods as well as the leaf and flower buds are eaten as "quelites", the greens traditionally consumed by indigenous people in Mexico (Bye 1981). "**Yiwa**" is the Mixtec term for quelite, and "**yiwa tinduva**" is the term for *Leucaena* edible greens. "**Yiwa tinduva**" are gathered from June to September, and more intensively during July and August (Fig. 3). The galls (locally called "**polochoco**"), which frequently develop on leaves and pods are consumed raw, roasted or boiled.

Immature seeds are the products most commonly consumed. They are eaten raw, roasted, milled and added to traditional chilli sauces, or cooked in stews. Seeds are gathered form November to February, when they are still immature. The seeds may be consumed just after gathering or stored. For storage, the seeds are ground into a paste, which is divided into smaller lots. These lots are dried to the sun, and then stored in plastic bags. They are hung on the wall or roof to prevent rodent attack. Also, the seeds are dried and salted, and this product for storage is called "**guajesquite.**" Guaje seeds are the only wild edible product which is stored for long term consumption by the Mixtec.

During the harvest season, "**yiwatinduva,**" raw or roasted pods and seeds of the red guaje are commonly sold in regional markets. After the harvest season the wild guaje edible products are substituted for those obtained from cultivat-

TABLE 6. EIGENVECTORS.

Characters	Principal components 1	2	3
Maximum seed length	−0.7112	−0.0253	−0.0550
Maximum seed width	−0.8796	0.1277	0.1130
Maximum seed thickness	0.4840	−0.4270	0.5907
Seed chamber length	0.8725	0.2034	0.0178
Seed chamber width	−0.7324	0.4739	0.0953
Septum thickness	0.7556	0.2305	0.4584
Maximum pod length	0.8426	−0.0503	−0.0698
Maximum pod width	−0.4757	0.7537	0.0227
Maximum pod thickness	0.8903	0.1901	−0.0516
Pod pedicle length	−0.5289	0.5225	0.3243
Pod margin width	−0.4765	−0.7143	−0.0775
Number of ovules	−0.6743	0.1369	−0.1679
Number of seeds	0.5670	0.2160	−0.6854
Number of aborted seeds	0.7340	0.3145	0.4028
Number of predated seeds	0.7314	0.2777	−0.3936

ed trees of *L. leucocephala* subsp. *glabrata* which yields pods throughout the year.

MANAGEMENT

There are three forms of management of *L. esculenta* subsp. *esculenta* by the Mixtec in La Montaña de Guerrero: cultivation, gathering from purely wild populations, and selective retention or tolerance of particular individuals in disturbed areas. Harvesting trees from wild populations is the most common form to obtain buds and pods of red guaje. Harvesting of wild trees

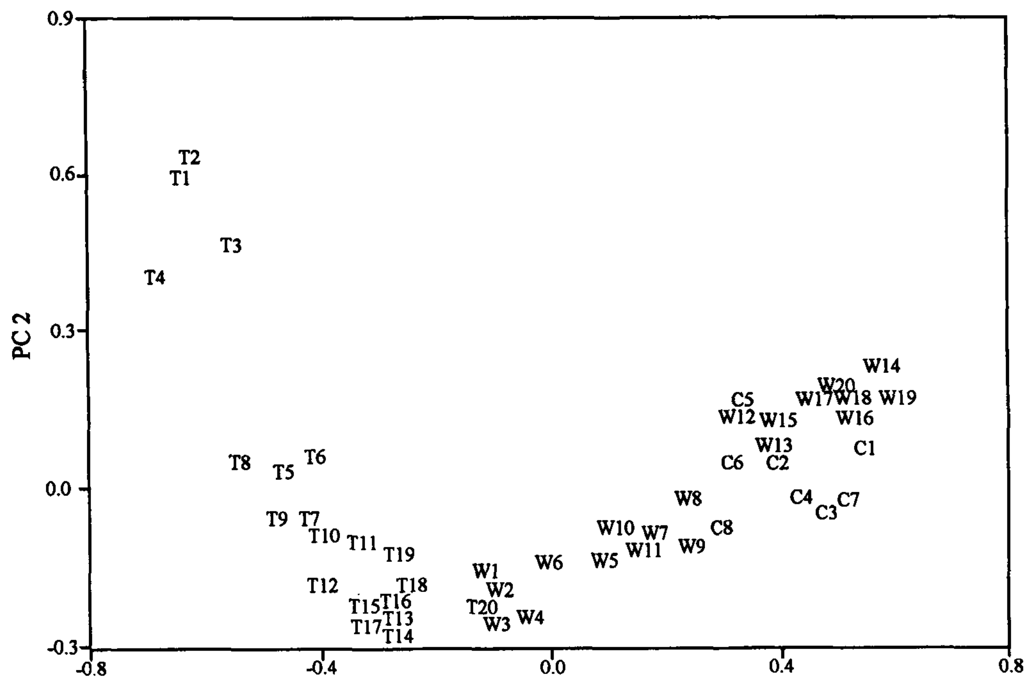

Fig. 4. Projection of the guaje trees in the space of the two first principal components. (W = wild, T = tolerated and C = cultivated trees.)

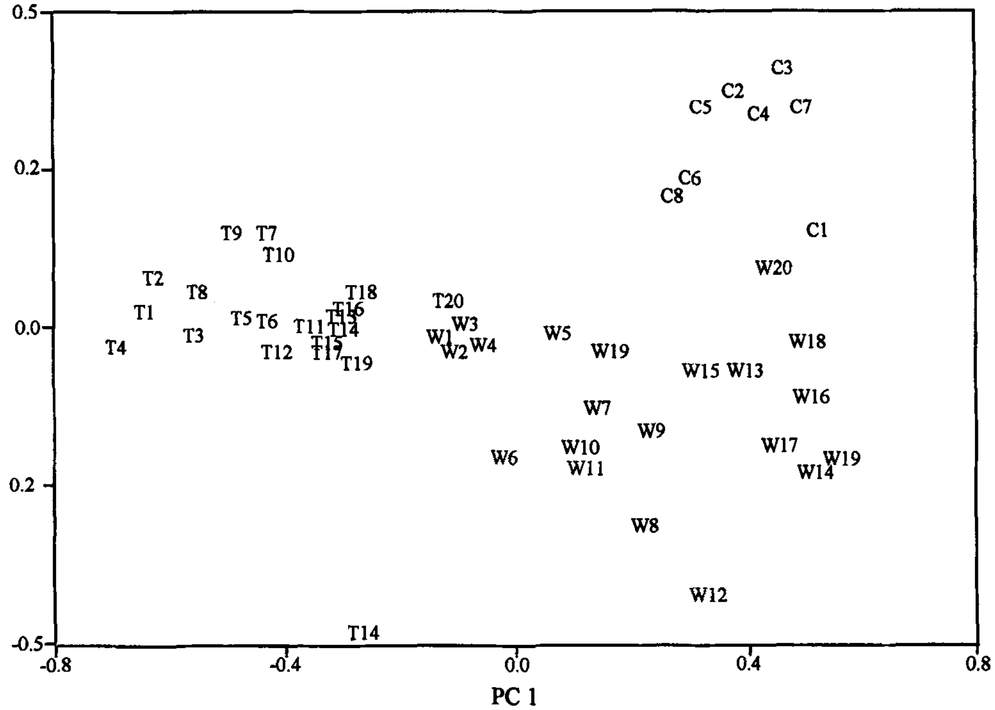

Fig. 5. Projection of the guaje trees in the space of the first and third principal components. (W = wild, T = tolerated and C = cultivated trees.)

is selective. The Mixtec harvest mostly the "guajes mansos" ("sweet guaje"). Occasionally they collect "bitter guaje" as well. They never harvest the "vomitory guaje." The Mixtec know exactly the places where the "best" trees can be found. This traditional knowledge is commonly shared among the members of the household and within the community. Thus, there are some wild trees which are preferred for harvesting. They are recognized by the presence of incisions on the stem which are made by people when climbing the trees for harvesting them.

Tolerance of individuals in disturbed areas consists in sparing the "sweet guajes" when clearing the forest for agriculture. During this practice, both vomitory and bitter guaje trees are generally cut down. Such practices are also carried out with other edible species such as *Pithecellobium dulce* (Roxb.) Benth. and *Prosopis laevigata* (Humb. and Bonpl. ex Willd.) M.C. Johnston.

TABLE 7. DISCRIMINANT FUNCTION ANALYSIS.

Discriminant function	Eigenvalues	Relative percentage	Canonical correlation	
1	4.08213	73.25	0.89623	
2	1.49056	26.75	0.77362	
Derived functions	**Wilks Lambda**	**Chi square**	**d.f**	**Sig. level**
0	0.0790054	96.453084	30	0.00000
1	0.4015157	34.675332	14	0.00164

Guaje cultivation includes planting trees in home gardens and corn fields as living fences, or on terrace borders. Cultivation involves two forms of artificial selection. First, the Mixtec select seeds which are considered the best for eating. They are obtained from both wild and cultivated trees. They are sown into seedbeds or planted directly in the fields or in the home gardens. Some weeks after being sown, the most vigorous seedlings are selected from the seedbeds and transplanted to fields. In the case of direct sowing, the less vigorous seedlings are eliminated in order to decrease their population density and resulting competition. These practices may represent a second form of artificial selection.

In La Montaña de Guerrero, *L. esculenta*

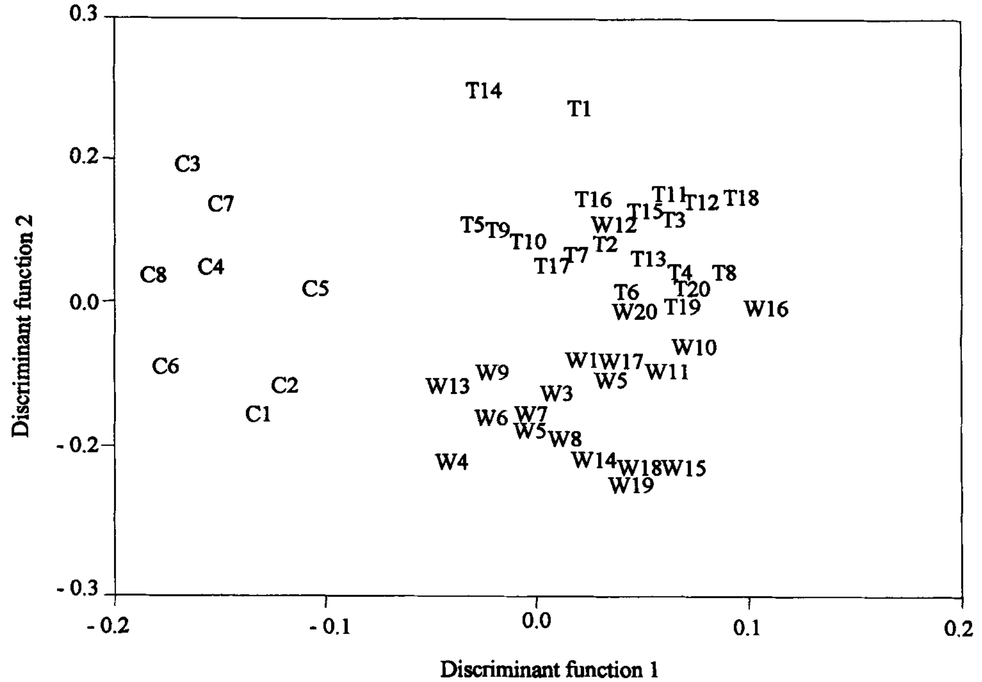

Fig. 6. Plot of guaje trees resulting from a discriminant function analysis. (W = wild, T = tolerated and C = cultivated trees.)

subsp. *esculenta* is never cultivated intensively. It is rather restricted to planting some individuals in home gardens. The Mixtec say that "it is not necessary to cultivate more red guajes because there are many trees available in the wild." In this area, the main source of guajes are the wild populations, especially those in which selective tolerance has created an abundance of desired phenotypes.

Patterns of Morphological Variation

The multivariate analysis of morphological variation generally reveals the grouping of the different tree samples according to the form of management. Principal component analysis (Tables 5, 6) clearly separates three groups of trees. Thus, in Fig. 4, the first principal component distinguishes two main groups of individuals. One group includes almost 80% of the wild guajes and all the cultivated trees while the other consists of all the tolerated individuals and approximately 20% of the wild ones. In Fig. 5, the first and third principal component discriminate three groups. One is formed by all the tolerated individuals and approximately 25% of the wild; a second is constituted by all the cultivated guajes, and a third group with the remaining wild individuals. Table 6 shows that in the first principal component, the variables related to seed and pod dimensions, as well as the number of predated and aborted seeds are the characters with a higher contribution to the variation ex-

Table 8. Classification of individuals into populations according to Discriminant Analysis.

Actual groups	Predicted groups: 1		2		3		Total	
	Num.	%	Num.	%	Num.	%	Num.	%
Wild	17	85	3	15	0	0	20	100
Tolerated	0	0	20	100	0	0	20	100
Cultivated	0	0	0	0	8	100	8	100

TABLE 9. RELATIVE IMPORTANCE OF CHARACTERS TO THE CLASSIFICATION OF POPULATIONS THROUGH DISCRIMINANT ANALYSIS.

	Discriminant value			
	Function 1		Function 2	
Character	b	b	b	b^2
Maximum seed length	−0.94392	0.89	0.23130	0.050
Maximum seed width	0.61594	0.38	1.38521	1.920
Maximum seed thickness	0.22587	0.05	−0.19564	0.040
Seed chamber length	−0.21501	0.05	0.65797	0.430
Seed chamber width	1.47044	2.16	0.10388	0.010
Maximum pod length	−0.36489	0.13	−2.21081	4.890
Maximum pod width	−0.81176	0.66	0.14924	0.020
Maximum pod thickness	−0.16997	0.03	−0.43848	0.190
Pod pedicle length	−0.47228	0.22	0.43892	0.190
Number of ovules	−4.68732	21.97	0.87630	0.770
Septum thickness	−0.41978	0.18	0.05944	0.004
Pod margin width	1.10423	1.22	−0.08743	0.010
Number of seeds	4.77531	22.80	−0.11530	0.010
Number of aborted seeds	2.62871	6.91	−0.19499	0.040
Number of predated seeds	0.59983	0.36	0.07232	0.010

plained. In the second component, the pod margin is the most important, while in the third principal component the greatest magnitude is given to seed number. The discriminant function analysis gives a better solution and shows three statistically different groups of trees according to management (Table 7). Such results corroborate those obtained under the principal component analysis. As can be seen from Fig. 6, the first discriminant function discriminate all the cultivated trees from the rest while the second discriminant function separates the tolerated from the wild trees. As shown in Table 8, there were no errors of classification in the case of cultivated individuals while only three wild trees were missclassified as tolerated individuals. The characters more relevant for discriminating cultivated individuals are mainly related to seed number. The characters more relevant for discriminating the wild individuals from the tolerated are mostly related to seed and pod size (Table 9).

The analysis of variance shows that pods and seeds of wild individuals are significantly smaller than those of the tolerated and cultivated individuals (Tables 10 and 11). Furthermore, this analysis reveals that the highest variation in pod and seed size is present in the cultivated sample while the variation is similar in both wild and tolerated populations (Fig. 7, 8).

DISCUSSION

The management of *Leucaena esculenta* subsp. *esculenta* by the Mixtec includes complementary forms of plant manipulation which are intended to assure a steady yield of edible products. Thus, in areas where wild resources are readily available, cultivation may have little im-

TABLE 10. ONE-WAY ANALYSIS OF VARIANCE FOR POD SIZE OF WILD, TOLERATED AND CULTIVATED TREES.

Sample	Average	95% Tukey HSD intervals for mean		Homogenous Groups	
Wild	21.4870	17.825692	25.148308	*	
Tolerated	27.6955	24.034192	31.356808		*
Cultivated	30.2525	24.463464	36.041536		*
Source of variation	Sum of squares	d.f.	Mean square	F-ratio	Sig. level
Between groups	599.1197	2	299.55987	3.282	0.0467
Within groups	4106.8507	4	91.26335		

TABLE 11. ONE-WAY ANALYSIS OF VARIANCE FOR SEED SIZE OF WILD, TOLERATED AND CULTIVATED TREES.

Sample	Average	95% Tukey HSD intervals for mean		Homogenous Groups	
Wild	0.47750	0.4330667	0.5219333	*	
Tolerated	0.65550	0.6110667	0.6999333		*
Cultivated	0.59625	0.5259948	0.6665052		*
Source of variation	Sum of squares	d.f.	Mean square	F-ratio	Sig. level
Between groups	0.3227404	2	0.1613702	12.006	0.0001
Within groups	0.6048575	45	0.0134413		

portance. In contrast, planting trees becomes important as long as wild trees are scarce or absent. In addition, tolerance as a form of in situ management of wild populations has been used to promote availability and increase numbers of guajes of better quality where cultivation is not well developed. This pattern of management forms part of a diversified strategy of subsistence which is common among indigenous peoples of Mexico and which takes advantage of all the available plant resources by integrating different forms of plant manipulation (Caballero 1994). As discussed by Hernández-X. (1993), this subsistence strategy represents an equilibrium between the availability of plant resources in the local environment and the technological abilities of the local human population.

As suggested by the results of the analysis of morphological variation, the management of *L. esculenta* subsp. *esculenta* by the Mixtec may involve a process of domestication. Artificial selection is likely occurring where the Mixtec identify those trees with bigger and better pods, and spare them when the forest is cleared. Another form of artificial selection may occur when seeds of the "best" individuals are planted morphologically in home gardens and corn fields. Principal component analysis clearly distin-

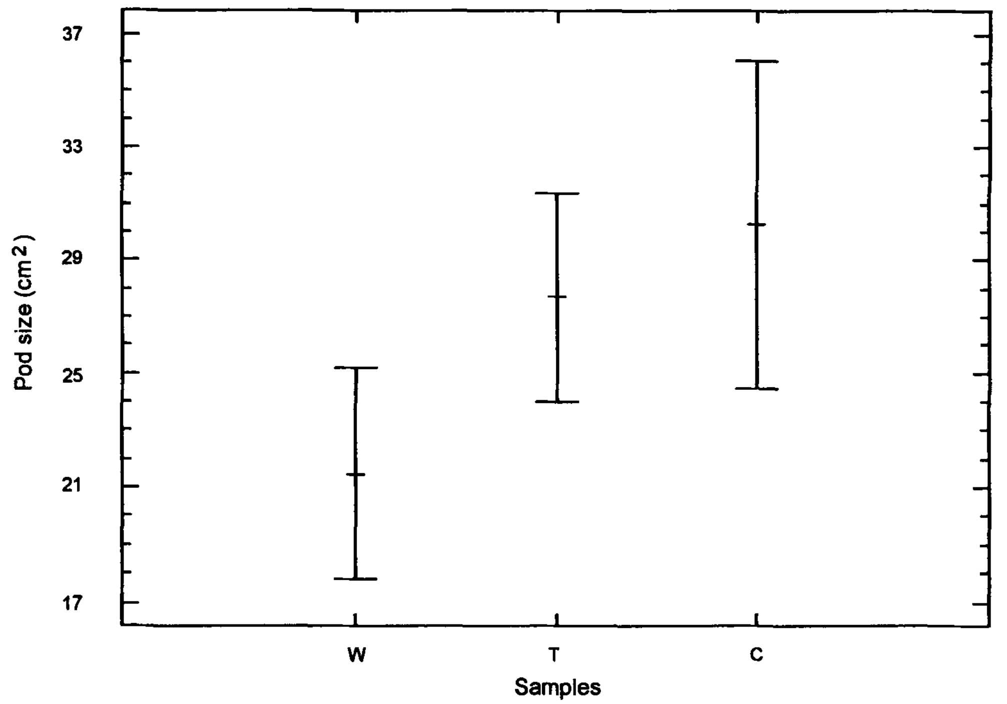

Fig. 7. Analysis of variance for pod size of guaje trees. Means and 95% Tukey HSD intervals for mean. (W = wild, T = tolerated and C = cultivated.)

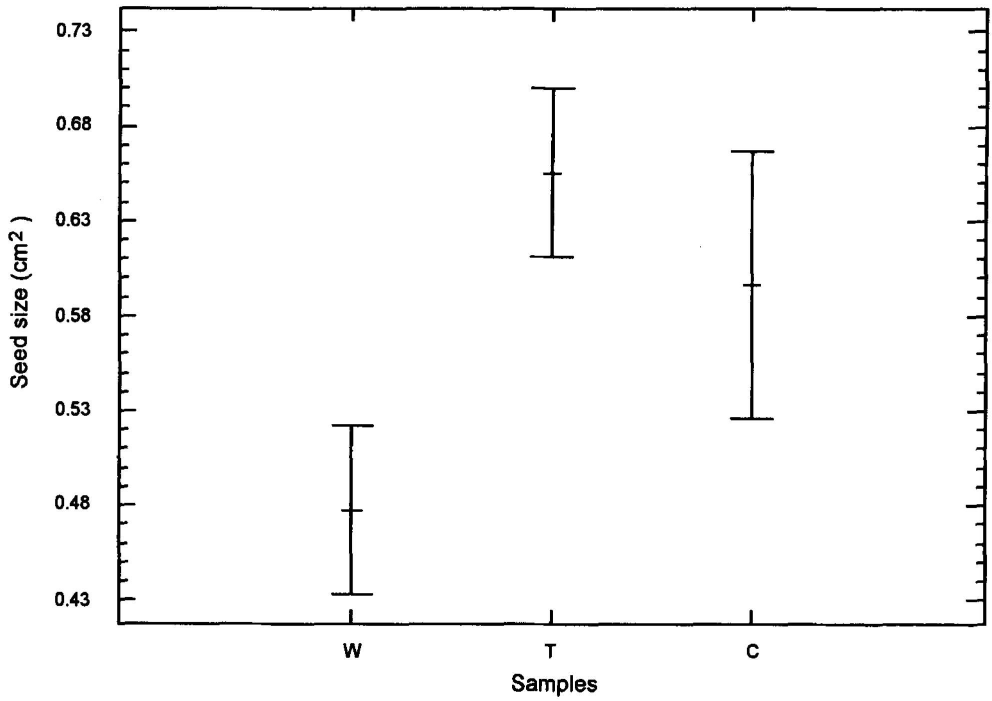

Fig. 8. Analysis of variance for seed size of guaje trees. Means and 95% Tukey HSD intervals for mean. (W = wild, T = tolerated and C = cultivated trees.)

guishes among individuals according to the form of management, wild, tolerated, or cultivated, under which they have groups. In addition, discriminant analysis demonstrated that there are significant differences between these populations.

As shown by both PCA and DFA, the tolerated trees form a well defined group. Although some wild trees are grouped along with the tolerated ones, they are those which present signs of having been frequently harvested. This suggests that the phenotypes selected in the tolerated populations occur naturally in wild populations, but at a lower frequency, and that artificial selection during selective sparing is directed to increase the frequency of the preferred phenotypes. Principal component analysis also distinguished some cultivated trees which are similar to wild guajes. Such individuals originated from local wild populations.

According to DFA, the first discriminant function indicates that the cultivated individuals have fewer seeds than the rest. On the other hand, the wild individuals tend to have smaller seeds and pods than both tolerated and cultivated individuals. This suggests that selection by local people seems to be directed toward obtaining trees which yield fewer but larger seeds.

The one-way analysis of variance was consistent with the results of multivariate analysis and confirms that the wild trees have significantly smaller pods and seeds than the tolerated and cultivated individuals. These results also confirm that there is an increase in size of pods and seeds in trees managed by humans. Wild and tolerated populations presented similar intervals of variation in pod and seed size. However, the sampled area of the tolerated population is much larger than that of the wild population. This may entail a reduction of variation in these characters in the tolerated population. This could be an effect of the selective sparing of desired phenotypes. In contrast, although comprising fewer individuals, the cultivated individuals sampled presented a wider interval of variation. This could be a result of the different provenance of these individuals.

Further research is needed to assess the genetic basis of the phenotypic variation found between the different populations studied. Since the samples were collected in different sites, it would be possible that the differences observed among wild, tolerated and cultivated populations might be a result, at least in part, of environmental factors. However, the presence of similar phenotypes in the three different sites suggests that morphological differences observed between wild and tolerated populations do have a genetic basis.

Studies on manipulation of wild plants (Alcorn 1981; Bye 1985, 1993; Casas, Viveros, and Caballero 1994) suggest that direct or indirect selection resulting from management of environment favorable to certain plants may have a significant impact on the genetic structure of plant populations. This might represent a route for plant domestication. In the case of *L. esculenta* subsp. *esculenta,* the results of morphological variation suggest that forms of in situ management such as selective tolerance may have effects altering the phenotypic structure of population. This also suggests that in situ management could alter the genotypic structure of population and therefore have evolutionary consequences. Considering the above, some forms of in situ management might be considered part of the domestication process. It is important to emphasize that in the form of in situ management examined in this paper, cultivation is not involved. Therefore, selective tolerance may represent a form of in situ domestication, in which successive generations of harvesting and sowing are not occurring.

Domestication in situ is an attractive model by which to investigate this process in perennial plants, such as *L. esculenta* subsp. *esculenta* which have outbreeding reproductive systems. In perennial plants the fixation of desired morphological characters may take a long time. From this point of view, it may be more plausible to increase desired phenotypes in outcrosser perennial plants by selective in situ sparing of the preferred phenotypes rather than bringing them into cultivation. With this procedure and the elimination of the undesired phenotypes, the frequency of crosses between desired phenotypes might be favored—at least in theory. Following this method may result in an increase in productivity and quality of non-timber resources as well as increasing the frequency of favorable phenotypes in the progeny. It is possible then, that in perennial outcrossers such as *L. esculenta* subsp. *esculenta* cultivation and selection might be more successful after in situ domestication.

Given its long history of use and management and its intensive present utilization, *Leucaena esculenta* may be considered a highly important plant resource for Mixtec subsistence. A similar situation occurs among other Mesoamerican Indian groups (Casas 1992; Vázquez 1986; Zárate 1982). Its quality as human food along with its use as fodder and fuel wood as well as its long history of human manipulation, could make *L. esculenta* a plant resource with an economic value as high as that of the widely known *L. leucocephala.* Production of better quality guajes for human food and for other purposes could benefit from assessing the morphologic variation resulting from the manipulation of this plant resource by indigenous people.

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LITERATURE CITED

Alcorn, J. B. 1981. Huastec noncrop resource management: implications for prehistoric rain forest management. Human Ecology 9:395–417.

Berlin, B. 1992. Ethnobiological classification. Principles of categorization of plants and animals in traditional societies. Princeton University Press, Princeton, New Jersey.

———, **D. E. Breedlove, and P. H. Raven.** 1974. Principles of Tzeltal plant classification. Academic Press, New York and London.

Bye, R. A. 1981. Quelites—ethnoecology of edible greens—past, present and future. Journal of Ethnobiology 1:109–123.

———. 1985. Botanical perspectives of ethnobotany of the Greater Southwest. Economic Botany 39: 375–386.

———. 1993. The role of humans in the diversification of plants in Mexico. Pages 707–731 *in* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, eds., Biological diversity of Mexico. Oxford University Press, New York, Oxford.

Caballero, J. 1994. La dimension culturelle de la diversité vegetalle au Mexique. Journal D'Agriculture Traditionalle et de Botanique Apliquee, nouvelle série 36:145–158.

Casas, A. 1992. Etnobotánica y procesos de domesticación en *Leucaena esculenta* (Moc. et Sessé ex A.DC.) Benth. MSc Dissertation. Facultad de Ciencias, Universidad Nacional Autónoma de México. México.

———, **J. L. Viveros, E. Katz, and J. Caballero.** 1987. Las plantas en la alimentación mixteca: una aproximación etnobotánica. América Indígena 47: 317–343.

———, ———, **and J. Caballero.** 1994. Etnobotánica mixteca: sociedad, cultura y recursos naturales en la Montaña de Guerrero. Instituto Nacional Indigenista-Consejo Nacional para la Cultura y las Artes. México.

Hernández-X, E. 1993. Aspects of plant domestication in Mexico: a personal view. Pages 733–753 *in* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, eds., Biological diversity of Mexico. Oxford University Press, New York, Oxford.

Hughes, C. E. 1993. *Leucaena* genetic resources. The OFI *Leucaena* seeds collections and a synopsis of species characteristics. Oxford Forestry Institute. University of Oxford, U.K.

Long, A., B. F. Benz, D. J. Donahue, A. J. T. Jull, and L. J. Toolin. 1989. First direct AMS dates on early maize from Tehuacán, Mexico. Radiocarbon 31:1035–1040.

MacNeish, R. S. 1967. A summary of the subsistence. Pages 290–231 *in* D. S. Byers, ed., The prehistory of the Tehuacan Valley. Volume one: Environment and subsistence. University of Texas Press, Austin, Texas.

Rohlf, J. 1993. Numerical taxonomy and multivariate analysis system for the IBM PC microcomputer (and compatibles). Version 1.8. Applied Biostatistics Inc., New York.

Smith, C. E. 1967. Plant remains. Pages 220–225 *in* D. S. Byers, ed., The prehistory of the Tehuacan Valley. University of Texas Press, Austin, Texas.

———. 1986. Preceramic plant remains from Guilá Naquitz. Pages 265–274 *in* K. Y. Flannery, ed., Guilá Naquitz. Academic Press, New York.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical taxonomy. The principles and practice of numerical classification. Freeman, San Francisco, California.

Sorensson, Ch. T., and J. L. Brewbaker. 1994. Interspecific compatibility among 15 *Leucaena* species (Leguminosae: Mimosoideae) via artificial hybridizations. American Journal of Botany 81:240–247.

Vázquez, M. C. 1986. El uso de plantas silvestres y semicultivadas en la alimentación tradicional en dos comunidades campesinas del sur de Puebla. BSc. Dissertation. Facultad de Ciencias, Universidad Nacional Autónoma de México. México.

Viveros, J. L., A. Casas, and J. Caballero. 1993. Las plantas comestibles y la alimentación entre los mixtecos guerrerenses. Pages 625–670 *in* E. Leff, E. and J. Carabias, coord., La dimensión cultural del desarrollo sustentable. Centro de Investigaciones Interdisciplinarias en Humanidades, Universidad Nacional Autónoma de México-Editorial Porrúa. México.

Zárate, S. 1982. Las especies de *Leucaena* Benth. de Oaxaca, con notas para la sistemática del género para México. BSc Dissertation. Facultad de Ciencias, Universidad Nacional Autónoma de México. México.

———. 1984. Taxonomic revision of the genus *Leucaena* Benth. from Mexico. Bulletin IGSM: 24–34.

———. 1987. Taxonomic identity of *Leucaena leucocephala* (Lam.) de Wit, with a new combination. Phytologia 63:304–306.

———. 1994. Revisión del género *Leucaena* Benth. de México. Anales del Instituto de Biología, Universidad Nacional Autónoma de México. Serie Botánica 65:83–162.

Zizumbo, D., and P. Colunga. 1982. Los Huaves. La apropiación de los recursos naturales. Departamento de Sociología Rural, Universidad Autónoma de Chapingo. Chapingo, México.