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ECOLOGY AND ETHNOBOTANY OF *ZEA DIPLOPERENNIS:* PRELIMINARY INVESTIGATIONS

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ABSTRACT - Investigations currently underway in the Laboratorio Natural Las Joyas indicate that the occurence of the endemic *Zea diploperennis* is intimately associated with disturbed and anthropogenic environments. Populations of this species appear to be healthier under conditions of active maize cultivation suggestiong that its survival may require such environmental conditions. In abandoned fields, *Z. diploperennis* dominates the early successional stages apparently giving way to other species in the later stages of succession. The largest population, which covers aproximately 320 hectares, exists under conditions of active maize cultivation where *Z. diploperennis* behaves as an integral part of a traditional agroecosystem in which hybridization, and perhaps introgression, take place, and in which the plant also serves as a very important source of fodder. The latter has been responsible in large part for its dispersal to other sites in the Sierra de Manantlan. We report also on the species' physical and biotic environmental context. Our studies call attention to the importance of humans in the present day success and apparent fitness of this species, as well as its association with prehistorically human-modified environments. This implies the need for conservation measures somewhat different to those commonly taken to conserve endemic species from advanced successional environments: the need to conserve the existing system of traditional land use and management under which it survives today.

KEY WORDS: *Zea diploperennis;* Ecology and ethnobotany of *Zea;* Maize ancestors.

INTRODUCTION

Ten years after the discovery and description of the endemic diploid perennial teosinte *Z. diploperennis* Iltis, Doebley and Guzman, and almost two years after the creation of the Sierra de Manantlan Biosphere Reserve there is still a need for ecological studies of the species to undestand how and under what environmental conditions it lives and determine what type of relationship exists between man and this primitive relative of maize. Assuring the survival of the species is mandated by the creation of the Sierra de Manantlan Biosphere Reserve where its habitat and surrounding ecosystems are now protected. Knowing how it survives in its natural habitat will thus help us to apply management techniques that will assure its continued existence. Our goal in this paper is to provide a first installment toward a basic description and discussion of the species' ecology (associated species and abiotic characteristics of its habitat) and ethnobotany (historical and current use by native inhabitants) in order to provide preliminary management recommendations.

Background

Zea diploperennis (or *milpilla* as the species is locally known) was first known to botanists from the site of La Ventana at the head of the valley of San Miguel, Sierra de Manantlan in 1977; although it was mistakenly thought to be another population of a similar species, *Zea perennis* (GUZMAN 1978a, 1978b). The new species was described in 1979 (ILTIS *et al.*, 1979) and three additional populations (Las Joyas, Manantlan and Rincon de Manantlan) were discovered in the following year (ILTIS 1980; GUZMAN 1982). The basic ecological traits of this endemic species were first pointed out by ILTIS (1980) in his description of the discovery of these populations and the importance of the species to science. In his description, he posed some basic questions regarding the origin and history of the species' endemism, the species' ecological strategy in regard to successional environments, and the species' seed diespersal mechanism. In relation to all three of the above, the basic questions surrounding each of these populations of the species can be posed in the following manner: How long has the species been present in Las Joyas, in San Miguel, and in Rincon de Manantlan and Manantlan? How did these populations arrive in

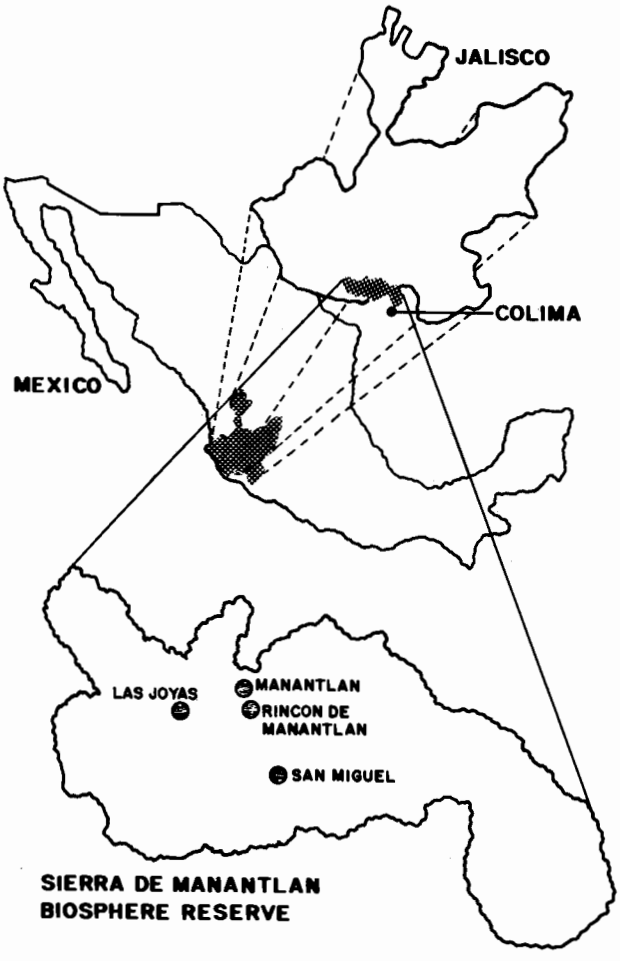


FIGURE 1 - Approximate locations of the four populations of *Zea diploperennis* in the Sierra de Manantlan Biosphere Reserve and its location in Mexico.

these locales; and are these populations naturally wild or anthropogenic? And finally, how and under what environmental conditions does the species exist today?

Z. diploperennis is confined to the Sierra de Manantlan of southwestern Jalisco, Mexico (Figure 1; Guzman 1982; Iltis 1980). All populations – 4 in all – are found between 19°38' and 19°29' N latitude and 140°12' and 140°18' W longitude, and between 1350 and 2440 meters above sea level.The population found at the lowest altitude, apparently recently planted, occurs near the settlement of Manantlan, and the highest, at the species' type locality of La Ventana – a mountain pass between the valleys of Cuzalapa/El Durazno and San Miguel. The populations at Las Joyas and Rincon de Manantlan are situated on predominantly southeast-facing slopes, the populations at San Miguel and Manantlan on southwest-facing slopes. This species is apparently a heliophyte like its congeners and its relatives in the genus *Tripsacum* (Wilkes 1972), producing dense stands in forest clearings that appear to have been opened principally by human activities for agriculture or grazing (cf. Guzman 1982; Iltis 1980). Clumps observed in areas of dense shade are relatively small and the stems definitely depauperate. The vegetation types surrounding the openings inhabitated by *Z. diploperennis* are pine, pine-oak, and cloud forest.

The populations vary widely in areal extent. The smallest is that found in Rincon de Manantlan which is comprised of less than one hectare. Approximately 40 hectares are inhabitated in Las Joyas and somewhat over 320 hectares in the valley of San Miguel (localities of La Ventana, San Miguel and El Pochite of the earlier literature). The populations in Rincon de Manantlan and Manantlan each consist of single stands. No field studies have yet been undertaken with these two populations because of their small size and due to the fact they were only recently introduced there. These two populations currently are used solely as a forage crop on which livestock is pastured. The two other populations, on the other hand, consist of numerous separate stands often with isolated clumps often encountered between the stands. The Las Joyas population is subdivided into 13 individual stands, these ranging in size from a fraction of a hectare to more than two hectares (Perez and Solis, in preparation). In all of the four known sites, the stands of *Z. diploperennis* are today encountered in what are or were agricultural plots planted principally to maize. Thus stands are found today in areas that were cultivated at some time during the last twenty years.

The situation at San Miguel is similar to that of Las Joyas, where the population does not exist as a single continuous stand but as a series of stands, some large or larger than five hectares. In contrast to the La Joyas population, the stands in San Miguel are actively "managed" as part of a three or more year rotation system of one year of cultivation followed by two or more years of fallow. During the two or more years of fallow the plant may be gathered as forage for the numerous pigs, donkeys, mules, and horses, or left standing to provide the principal species for pasturing cattle and beasts of burden. The seeds of the milpilla are widely distributed by cattle as indicated by the isolated clumps noted along cattle trails. This is probably due to the cattle freely grazing the stands in

fallow as well as those under cultivation after the maize has been harvested (in late December) when the seeds of *Z. diploperennis* are fully mature. However, the seeds do not apparently survive the passage through the digestive tract of pigs or of Equidae. According to the residents of San Miguel, the plant provides such excellent forage they are prompted to scatter the seeds in areas where the stands are thin, or the clumps are dispersed or absent.

The populations at Rincon de Manantlan and Manantlan are relatively dense individual stands of small size subject to active or passive grazing pressures. The species at Las Joyas is most common on the sites of abandoned agricultural parcels, of both slash and burn and plowed fields, which in the past have also been subject to grazing. The San Miguel population is subject to a more active managment cycle of slash and burn cultivation in which the plant may be cutback twice or more (or left as a seed parent) when the land is under cultivation, as well as being grazed annually.

METHODS

The ecological studies of the plant and its habitat took place entirely in vegetation of abandoned or human-maintained locales during November and December of 1988. Data collection was conducted using one meter square quadrats in six stands in various stages of old-field succession ranging from fields planted to maize during the year of sampling to 15 years after the field had been planted to maize. Six stands were sampled, three in the San Miguel population and three in the Las Joyas population. The two populations were surveyed by stratified random samples: randomized within a stand of a particular successional stage (one year, five years, 10 years, etc. since it was last cultivated) and stratified according to time since the site was last cultivated. The three stands sampled in San Miguel represent the year of initial disturbance, and the ensuing two years. Parcel 1 is that currently under cultivation, Parcel 2 represents the first year of fallow, Parcel 3 two years following cultivation. The three stands sampled in the Las Joyas population represent longer periods of secondary succession following cultivation; five years in the case of Las Playas, ten years after cultivation in the case of El Huiscorol, and 15 years in the case of Los Asoleaderos.

In order to get some idea of how the field had been maintained over the years, observations of a general nature were made for each of the various stands sampled: when was the field last planted and how it been tilled, whether fertilizer and/or herbicide had been applied, whether or not it had been grazed, when *Z. diploperennis* first appeared in the fields, and when and from what type of vegetation the studied parcel of land was first cultivated.

Observations made in each of the quadrats were of a more quantitative nature. Exposure, slope, soil depth and compaction, as well as percent of the total area clear of vegetation, were measured in all of the quadrats in San Miguel. Soil compaction was not recorded in the stands studies in Las Joyas. Number of stems (ramets) of the milpilla *(Z. diploperennis),* percent cover, and height of the tallest stem were observed in each of the quadrats studied in the San Miguel population. Stem height was not measured in individual quadrats in the Las Joyas population but determined from a number of randomly selected stems in each of two stands. Seed production was estimated for each stand based upon a) a randomly selected sample of stems, b) an estimate of the number of female inflorescence per plant and, c) the average number of seeds in a single female inflorescence. An evaluation of the damage to the stems of *Z. diploperennis* and cause of damage was also made in each quadrat. Because the milpilla is known to hybridize somewhat spontaneously with maize, a special effort was made to search for hybrids in each quadrat. All vascular plant taxa were also noted within each quadrat, this on a presence/absence basis.

In seeking to understand how the milpilla is and has been associated with humans, we conducted interviews with the native inhabitants to obtain a generalized description of the plant's uses and its history at each locale. Remembering that all extant populations "occur in or near human agricultural habitations" (Iltis 1980:21), we attempted to determine the time depth of human occupation at each locale. Interviews with local people provided an idea of the historic occupation as well as, in some cases, whether archaeological material had been encountered in the vicinity. Both men and women were interviewed where possible, and a number of individuals were interviewed more than once to corraborate responses given earlier. In addition to these interviews, on the ground reconnaissance provided a collection of archaeological diagnostics that have been used here to indicate the time depth of human occupation in the vicinity of the San Miguel and Las Joyas populations.

TABLE 1 - *Species encountered in the quadrats of the two largest populations of* Zea diploperennis *in the Sierra de Manantlan.*

Family	Genus/Species	Las Joyas			San Miguel		
		P	H	A	1	2	3*
Amaranthaceae	*Amaranthus hybridus*				x		
Amaryllidaceae	*Bomarea hirtella*				x	x	x
	Hymenocallis sp.	x	x	x			
Aristolochiaceae	*Aristolochia pentandra*					x	x
Buddleiaceae	*Buddleia parviflora*		x		x		
	B. sessiliflora	x	x		x		x
Cannaceae	*Canna indica*				x		
Capparidaceae	*Cleome speciosa*				x		
Caryophyllaceae	*Cerastium sinaloense*	x	x	x			x
	Drymaria sp.		x		x	x	x
Commelinaceae	*Commelina tuberosa*	x	x	x	x	x	x
	Tripogandra disgrega		x		x	x	x
Compositae	*Ageratum houstonianum*				x	x	x
	Baccharis heterophylla	x					
	Bidens mollifolia				x	x	x
	Cirsium jaliscoense	x	x	x			
	Cosmos carvifolius	x					
	Dahlia coccinea		x	x		x	
	Elephantopus mollis		x				
	Erigeron longipes	x	x	x			
	Eupatorium sp.				x		
	Gnaphalium attenuatum			x			
	Jaegeria hirta	x	x	x	x	x	x
	Jaegeria macrocephala				x	x	
	Melampodium perfoliatum						x
	Melampodium tepicense						x
	Perezia sp.					x	
	Senecio salignus	x	x	x			
	Sigesbeckia agrestis				x		
	Stevia ovata	x	x				
	Tagetes filifolia	x					
	Tagetes remotiflora				x	x	x
	Trigonospermum melampodioides		x			x	x
	Verbesina greenmanii				x	x	x
	Viguiera ensifolia				x	x	x
	Viguiera sp.				x	x	x
Convolvulaceae	*Ipomoea* sp.				x	x	x
	Quamoclit hederifolia				x	x	x
	Cuscuta corymbosa				x		x
Cucurbitaceae	*Cyclantera multifoliola*			x			
	C. tamnoides	x	x	x	x	x	x
	Echinopepon racemosus				x		
	Sicyos angulata	x	x	x	x	x	x
Cyperaceae	*Cyperus hermafroditus*				x	x	x
Dioscoreacea	*Dioscorea jaliscana*				x	x	x
Equisetaceae	*Equisetum* sp.	x					
Euphorbiaceae	*Acalypha* sp.	x				x	
Geraniaceae	*Geranium antisepalum*	x	x		x	x	x
Gramineae	*Cenchrus echinatus*				x		
	Chaetium bromoides						x
	Cynodon dactylon		x				
	Eragrostis mexicana				x		
	Festuca breviglumis	x	x	x			
	Lasiacis procerrima				x		
	Muhlenbergia diversiglumis					x	
	Oplismenus burmannii				x	x	x

TABLE 1 (continued)

Family	Genus/Species	Las Joyas			San Miguel		
		P	H	A	1	2	3*
	Panicum parviglume		x	x	x		
	Paspalum squamulatum	x	x	x	x	x	x
	Setaria geniculata				x	x	x
	Setaria scandens				x		
	Sporobolus indicus	x	x	x			
	Trachypogon montufari	x					
	Trisetum deyeuxioides	x	x				
	Zea diploperennis	x	x	x	x	x	x
	Zea mays				x		
Hydrophyllaceae	*Phacelia platycarpa*	x	x	x			
Labiatae	*Hyptis* sp.	x	x	x	x		x
	Salvia riparia	x	x	x	x		x
	Salvia sp.	x	x	x	x	x	x
	Stachys agraria	x	x	x			
Leguminosae	*Acacia angustissima*	x	x	x	x	x	x
	Aeschynomene villosa				x	x	x
	Cologania broussonetii	x	x	x	x	x	x
	Crotalaria longirostrata	x			x	x	x
	Crotalaria mollicula				x	x	x
	Dalea polystachya	x			x		x
	Desmodium aparines				x	x	x
	Desmodium skinneri var *flavovirens*				x	x	
	Desmodium sp.				x	x	x
	Lupinus elegans	x	x	x			
	Mimosa galeottii				x		x
	Phaseolus coccineus	x	x	x	x	x	
	Phaseolus vulgaris				x	x	x
	Senna leiophylla				x	x	x
	Trifolium amabile	x	x	x			
Liliaceae	*Echeandia* sp.	x	x	x			
Lobeliaceae	*Lobelia laxiflora*				x		
	Lobelia sp.				x	x	
Malvaceae	*Anoda cristata*				x		
	Kearnemalvastrum subtriflorum				x		
	Sida acuta						x
	Sida barclayi	x	x	x	x	x	x
Menispermaceae	*Cyssampelos pereira*					x	
Onagraceae	*Lopezia racemosa*	x	x	x	x	x	x
Oxalidaceae	*Oxalis corniculata*	x	x	x		x	
	Oxalis sp.	x	x	x			
Passifloraceae	*Passiflora* sp.				x	x	x
Polygonaceae	*Rumex crispus*	x	x	x			
Polygalaceae	*Monnina wrightii*						x
Ranunculaceae	*Clematis dioica*	x	x	x			x
	Ranunculus petiolaris	x	x	x			
	Thalictrum pringlei				x	x	
Rosaceae	*Alchemilla* sp.	x					
	Rubus adenotrichos		x		x	x	
	Rubus coriifolius	x	x				
Rubiaceae	*Crusea longiflora*				x	x	x
	Richardia scabra	x	x	x	x	x	x
	Crusea sp.				x		x
	Didymaea alsinoides			x			
Scrophulariaceae	Unknown species		x		x	x	x
	Castilleja arvensis				x		
Solanaceae	*Jaltomata procumbens*				x		

TABLE 1 (continued)

Family	Genus/Species	Las Joyas			San Miguel		
		P	H	A	1	2	3*
	Lycianthes sp.	x					
	Physalis sp.				x	x	x
	Solanum americanum			x	x	x	x
	Solanum appendiculatum		x	x			
	Solanum guerreroense	x	x	x			
	Solanum torvum				x	x	
Sterculiaceae	*Melochia nodiflora*				x	x	x
Tiliaceae	*Triumfetta semitriloba*	x	x		x	x	
Umbelliferae	*Eryngium ghiesbreghtii*	x					
	Rhodosciadium pringlei	x					
Verbenaceae	*Priva aspera*				x	x	x
	Verbena carolina	x		x			
Violaceae	*Viola grahami*	x	x	x			

* In Las Joyas, P refers to Las Playas, A to Los Asoleaderos, and H to El Huiscorol; in San Miguel, 1 refers to Parcela 1, 2 to Parcela 2, and 3 to Parcela 3.

** The species present on this list are vouchered by specimens on file in the Herbarium of the Laboratorio Natural Las Joyas (ZEA) in El Grullo, Jalisco, Mexico.

Ecology of *Zea diploperennis*

The stands in Las Joyas have all been subject to fairly intense agricultural practices, at least during the last five years predating the establishment of the *Estacion Cientifica Las Joyas* by the University of Guadalajara in 1985. These practices included application of fertilizer, herbicide and pesticide. In the majority of the tracts sampled, the vegetation was most likely cloud forest prior to cultivation (SÁNCHEZ-VELÁSCHEZ 1988). In contrast, the sampled stands in San Miguel have never been subject to fertilizer application and only recently (the last three to five years) to the application of herbicide. It would appear that the original vegetation in San Miguel was cloud forest also, at least in the case of the three stands sampled. Here too the vegetation is now composed principally of secondary species, and apparently has been so for some time.

Within the 325 quadrats sampled in Las Joyas and San Miguel, a total of 124 species of vascular plants were encountered (Table 1). The stands in San Miguel contained the greatest number of species with 85, representing 34 families, while those of Las Joyas contained slightly less with 67 species, these representing 26 families. The vast majority of species are herbaceaous perennials. Sørensen's index of similarity (MUELLER-DOMBOIS and ELLENBERG 1974: 211-243) was calculated to compare the flora of the two populations. A value of 51% indicates that a relatively large number of species were encountered in both San Miguel and Las Joyas. Only 12 species were common to all the stands sampled in Las Joyas and San Miguel (Table 1).

The number of species encountered in the six sampled stands show a significant relationship with the time the site has been abandonded ($r = -0.8$; $p<.04$; Figure 2), indicating a significant decrease in species number with increase in time since abandonment. Although we expected a relationship between annuals and woody perennials, viz., a greater number of annuals in the stands in San Miguel than in Las Joyas and fewer woody perennials at San Miguel than at Las Joyas, differences were not significant ($X^2 = 0.88$, df = 5, n.s.). The results were ambiguous in the case of herbaceous perennials. While there is reason to expect an increasing number of herbaceous perennials with longer adandonment time, the results demonstrate a suggestive though nonsignificant association ($X^2 = 17.51$, df = 10, $p < 0.1$) in which a greater number of herbaceous perennials were encountered in the stands in Las Joyas (i.e., later) and a lower than exected number in San Miguel (i.e., in the earliest stages of secondary succession). Greater attention to one of the more common annual species, e.g., *Jaegeria hirta,* (second only to *Z. diploperennis* in frequency of occurrence in all the stands), a diminutive Compositae, supports the belief that species replacement, particularly of annuals, is occurring over time (Figure 2).

Patterns of species association also proved to be

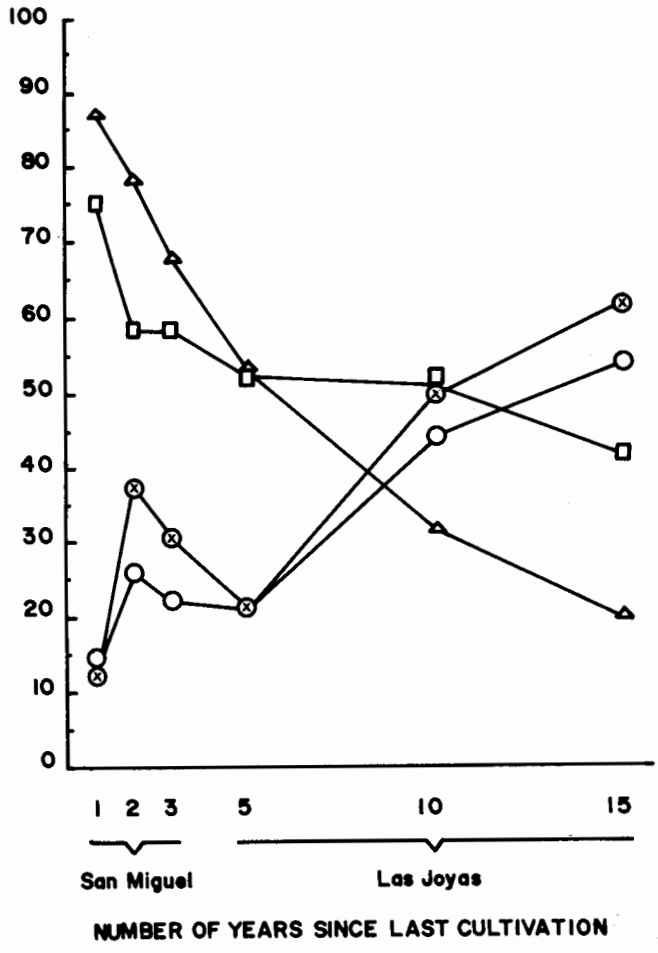


FIGURE 2 - Diagram showing changes in the vegetation in the stands of *Z. diploperennis* sampled in San Miguel and Las Joyas. ⊗ average percent cover of *Z. diploperennis* per quadrat; ○ average number of stems of *Z. diploperennis* per quadrat; □ total number of species per stand; △ percent of quadrats per stand containing *Jaegeria hirta*.

more or less as expected (Table 2). The stands in San Miguel, representing old-field situations with short abandonment times, proved to have a larger number of significant positive and negative species associations than in Las Joyas, though the species show no tendency to form species' groups. The situation al Las Joyas illustrates something quite different. Here fewer significant positive and negative species associations present themselves and these exhibit a tendency toward the formation of two species groups, one, composed of 20 species, focused around a significant positive association between *Z. diploperennis* and *Phaseolus coccineus,* the other of 24 species, centered around a strong association of *Geranium antisepalum, Erigeron longipes,* and *Cyclantera tamnoides*.

TABLE 2 - *Number of species in the San Miguel and Las Joyas populations showing positive or negative associations with other species.*

	Number of significant species correlations			
	positive association		negative association	
	$p < 0.05$	$p < 0.01$	$p < 0.05$	$p < 0.01$
San Miguel	88	32	34	15
Las Joyas	49	24	26	4

Z. diploperennis showed remarkably strong association in its behavior with regard to abandonment time (Figure 2; Table 3). The longer the site's abandonment time, the greater the average percent cover and mean number of ramets per quadrat ($r = 0.96$, $p = 0.003$; $r = 0.87$, $p = 0.025$ respectively). Female inflorescence number varied positively with stem height ($r = 0.89$, $p = 0.04$). Seed number per female inflorescence showed little variation across stands or between populations. While we might attribute greater plant height and increased female inflorescence production to abiotic factors (see Table 4) such as soil depth or compaction, slope, exposure, or percentage of the quadrat clear of vegetation, only the latter (and this in San Miguel) showed significant relationship with maximum stem height ($r = -0.17$, $p < 0.03$), and it explains very little, viz. only 3%, of the variation in stem height.

Within populations, the stands having the shortest abandonment times in each locality (Parcel 1 in San Miguel, and Las Playas in Las Joyas, Figure 2) exhibited the fewest number of ramets per quadrat ($F = 31.5$; $p < 0.001$), the lowest percent cover within the quadrat ($F = 39.8$; $p < 0.001$), and the shortest maximum stem height ($F = 102.0$; $p < 0.001$). We attribute this to the "pruning" of *Z. diploperennis* in the case of Parcel 1, and to very recent grazing in the case of Las Playas. The two older stands in each population showed no significant difference in number of ramets per quadrat, percent cover or maximum stem height either between or within populations. Within populations there is a very suggestive trend for the older stands to have a greater average number of ramets per quadrat and for *Z. diploperennis* to exhibit greater coverage (Table 3).

Herbivory was uniformly noted in all stands. Damage was most frequently noted on only a few leaves per plant and this due principally to insects. In none of the six stands was the damage particularly great. In only one stand, this in Asoleaderos, was vertebrate damage particularly common. Here the

TABLE 3 - *Characteristics of* Zea diploperennis *in the six study stands in Las Joyas (LJ) and San Miguel (SM).*

Stand	SM Parcel 1	SM Parcel 2	SM Parcel 3	LJ Las Playas	LJ Huiscorol	LJ Asoleadores
Ramets per	14.2*	26.1	22.4	21.7	44.4	54.2
quadrat	1.6	2.0	2.2	4.2	3.6	3.2
Percent	12.4	37.9	30.3	21.7	50.0	62.0
Cover	1.2	3.1	3.2	3.9	3.9	3.0
Maximum	93.6	265.9	257.9	131.3	–	243.7
Stem Height (cm)	7.9	5.9	5.3	5.8		5.2
Pistillate	5.2	22.1	13.2	9.2	–	16.0
Inflorescences/plant	0.7	5.8	1.9	2.8		2.8
Seeds/	5.4	5.6	5.0	4.0	–	5.5
Inflorescence	0.4	0.3	0.3	0.0		0.6

* Mean and standard error.

TABLE 4 - *Abiotic characteristics of the six study stands.*

Stand	SM Parcel 1	SM Parcel 2	SM Parcel 3	LJ Las Playas	LJ Huiscorol	LJ Asoleadores
Soil	33.4*	37.8	40.1	52.1	31.2	62.6
Depth	2.4	3.1	3.2	3.1	3.3	3.7
Slope	13.8	14.9	12.8	7.1	8.3	8.5
	1.1	1.5	1.1	0.6	0.8	0.8
Exposure**	185.4	226.1	237.8	190.8	180.9	131.1
	5.4	4.5	6.9	6.2	7.2	14.2
Soil	2.6	1.7	1.5	–	–	–
Compaction	0.1	0.1	0.1			

* Mean and standard error.
** North is 0.0, south is 180.0.

leaf sheaths as well as the bracts enclosing inflorescences were torn, apparently to gain access to the seeds (probably small rodents; E. SANTANA C. pers. comm.) or to the insects present in the female inflorescence clusters (in this case probably by birds, see BEDOY 1988).

In each of the six stands, the milpilla almost uniformly exhibited near dominance. Only in Asoleaderos is there any obvious indication of encroachment by trees which might threaten *Z. diploperennis* with shading. In Parcel 2 and 3 in San Miguel, the milpilla forms nearly inpenetrable thickets and though an occasional tree may be left by the cultivators, their affect on the apparent dominance of this teosinte seems slight in these short intervals of "fallow".

While the stands in Las Joyas seem to be tenanciously holding their own, we can assume that with time these dense stands will slowly give way to the invasion of longer-lived, shade-producing species. We have seen this to be true of the stands in San Miguel where the inhabitants have discontinued their use of parcels for 30 years or more thereby allowing invasion and resprouting of trees and shrubs with a subsequent loss of *Z. diploperennis'* habitat.

At the present time, it might appear that the more successful population from a conservation standpoint is that of Las Joyas because of its higher density of ramets, greater average coverage, and more or less equivalent production of seed. However, we contend that this is probably not the case and that our results provide only half the story (see HARPER 1977; SILVERTOWN 1982). First, the increasing density of the stems noted with abandonment time is most likely due to increased production of ramets by a single genet, much like as been noted in other rhizomatous species (HARPER 1977:553; HARTNETT and BAZZAZ

1985). Second, and assuming the first to be true, percent coverage is linearly associated with ramet number and most likely reflects increased competition, first among genets and later among ramets with longer periods of abandonment (MADDOX *et al.*, 1989). Third, average maximum stem height is strongly associated with average number of female inflorescences per plant suggesting that the cost of investing in taller stems is repayed in increased female fitness as well as that of male fitness (cf. BURD and ALLEN 1988), and this, will probably be even greater under situations of more numerous genets (i.e. in the earlier stages of succession) than ramets (later successional stages) where there is an increased probability of outcrossing (HARPER 1977: 215-219, 549-564).

Ethnobotany of *Zea diploperennis*

The short description which follows is an attempt to clarify the modern-day relationships between the populations of *Z. diploperennis* in regard to the questions posed above on whether the populations are naturally wild or anthropogenic.

Paulino Terriques of Ahuacapan, who was the onetime caretaker of the land that is now the Las Joyas Scientific Station, offers two accounts of the history of the milpilla in Las Joyas. His first version suggests that the population may be indigenous, not recently introduced. He indicated that *Z. diploperennis* was present in Las Joyas at the time the Hacienda Ahuacapan was dispersed. At this time, ca. 1925, he was commissioned to take care of this small landholding at Las Joyas then owned by M. Valencia. At that time the land was being cropped and used to pasture cattle.

Paulino's second version is quite different and less credible because it does not agree with the descriptions given by other and perhaps more reliable informants. This version indicates that the seeds of *Z. diploperennis* were brought in to be planted as a forage crop for the cattle being pastured in and around Las Joyas. The seed was apparently gathered in Rincon de Manantlan for this purpose. The other informants, Jose Cruz and Jose Arias, from Las Joyas and Rincon de Manantlan respectively, have indicated that the seed of *Z. diploperennis* was gathered in Las Joyas and taken to both Rincon de Manantlan and Manantlan, and perhaps even to San Miguel, to be planted for forage. However, other informants from Rincon de Manantlan, as well as the late Jose Arias, all agree that the seed was brought in to be planted as a forage crop and that it came from Las Joyas. Moreover, all informants from San Miguel have indicated that the plant has "always" been there (which according to the informant's ages, between 40 and 70, plus that of their fathers [ca. 50] would take us as far back as the turn of the century). There is only one shred of doubt that the population in San Miguel is nonindigenous. This doubt stems from information provided by the present-day caretaker of Las Joyas; Jose Cruz. This informant, who arrived in the region 35 years ago, and has spent the last 20 years in Las Joyas, indicates that during the early 1960's, a villager from San Miguel made a part-time living gathering and selling seed of the milpilla. This individual apparently sold a liter of *Z. diploperennis* seeds for few centavos, carrying it from Las Joyas to both San Miguel and Rincon de Manantlan. There is some doubt that the seed was taken from Las Joyas to San Miguel because all except one of the persons interviewed in San Miguel agree that the plant has always been present in the valley of San Miguel.

In sum, we believe that there can be little doubt that the populations in Manantlan and in Rincon de Manantlan are non-native, i.e., seed most likely was brought in and planted as forage, probably from Las Joyas (see KATO and LOPEZ, this volume). There is less security about the Las Joyas and San Miguel populations though the majority of present-day evidence argues in favor on them being indigenous.

The age of the *Z. diploperennis* - human association

ILTIS (1980) called attention to the fact that the current distribution of *Z. diploperennis* is associated with present-day agricultural settlements. He points out that where one finds agricultural settlements at high elevations in the Sierra de Manantlan today, one also encounters the milpilla. Realizing now that the population from Manantlan and Rincon de Manantlan to be recently planted we focus solely on the question of temporal association in the Las Joyas and San Miguel localities.

Our field studies of these populations included on-the-ground reconnaissance for indications of prehistoric occupation and in both cases, prehispanic occupation of these locales is indicated. Ceramic sherds provide the best evidence for temporal definition of prehistoric occupation. In other cases, the absence of ceramics and the absence of obsidian artifacts, particularly prismatic blades, may suggest preceramic occupation.

Archaeological materials from the San Miguel locality indicate that the valley, and most likely the site of the pueblo itself, has been occupied since the Late

Preclassic (ca. 300 B.C. - A.D. 300). The diagnostic materials encountered are of Tuxcacuesco Red Ware and Tuxcacuesco Unpolished Utility Ware (KELLY 1949). Apparently, the site of current occupation was also occupied later during the prehispanic period. Autlan Polychrome and Altillos Red ceramic wares (KELLY 1945; 1949) and the prismatic blade fragments and projectile points of obsidian encountered are all characteristic of the Autlan and Toliman Phases (ca. A.D. 1200 - 1521). It is presently unknown whether this locality has been occupied continuously since the Conquest.

In Las Joyas we find evidence suggesting a more temporally continuous prehispanic occupation of the area. The presence of Autlan Red Ware indicates that this locality was occupied during the Postclassic horizon (Mylpa and later Autlan Phases); A.D. 900 to 1521. The presence of what very likely is a fragment of an Autlan Polished Orange Ware bowl suggests the area was probably also occupied during the Late Classic horizon (Cofradia Phase, A.D. 600 to 900). Additional finds including various figurines, and what may be Tuxcacuesco Red Ware Sherds, suggest a Late Preclassic (300 B.C. - A.D. 300; Tuxcacuesco Phase) horizon occupation as well. One low-temperature fired animal figurine in this collection may resemble one recently encountered in stratified deposits on the coast of Jalisco where it was recovered below Tuxcacuesco Phase ceramics (J. Mountjoy pers. comm.). Within the area known as Las Playas in the Las Joyas locality we also find an area of occupation which contains no ceramic material, no obsidian, only flaked-stone debitage. Although this might represent little more than a simple hunting or plant processing station occupied only seasonally and be quite recent within the prehispanic era, it could equally represent the preceramic horizon, potentially as early as 2500 B.C.

Based on the above, one can reasonably assume that *Z. diploperennis* may have been associated with anthropogenic environmental perturbation for the last 2,000 years, possibly longer. However, without additional archaeological investigation, we can be certain only that humans have been occupying these localities for this period of time; we can not be certain that *Z. diploperennis* has also been present at these sites for the same amount of time. We can do little more than speculate at the present time that prehistoric human intervention, had it been present at the outset (i.e., since the end of the Pleistocene), has very likely helped the species by providing open habitats for colonization, much like it does today. What we do not know yet is the time of man's first intervention. This question, and that of whether humans have been using the plant as they are today, will remain unanswered until archaeological work can focus on these problems.

Utilization of the *Zea diploperennis* today

Utilization of the milpilla by the inhabitants of the Sierra de Manantlan falls into two basic categories, fodder and maize "improvement".

The use of the species for forage has been responsible for establishing the population in Rincon de Manantlan as well as for Manantlan, and perhaps in other localities as well. For example, a small population located on the trail from La Ventana to El Durazno and Cuzalapa established itself after being brought from San Miguel by cattle as indicated by numerous seeds found germinating in dung piles. Indeed, the people residing in San Miguel indicate that the milpilla is a much more productive forage crop than any grass they have planted, e.g., *Panicum maximum*. Though probably a relatively recent practice, the natives of San Miguel foster the growth of *Z. diploperennis* in their agricultural fields to assure additional forage for the animals left to graze in the fields after harvest. Many go so far as to scatter the seed in their fallows in order to maintain sufficient forage during the years of fallow provided most parcels.

A second use the people of San Miguel have found for *Z. diploperennis* is that of hybridizing it with their traditional maize races (probably Reventador and Tabloncillo). Their reason for this apparently is to induce greater productivity and impart resistance of their maize to certain pests as well as purely out of curiosity. This is conducted in their slash and burn plots (locally known as *coamiles* because they are planted using a digging stick, *coa)* that are planted to maize usually once every three years. The fields have never been plowed, although there is now talk of introducing the plow into some of the few level areas. Only during the last five years have they begun to use herbicide, this the only chemical applied to their fields. During the first year the area to be planted is cleared of trees, shrubs and undergrowth which is left to dry so that it can be burned. When the first rains come, usually in the month of June, the parcel is planted with a digging stick. Harvest takes place near the end of the month December.

Hybridization of maize and *Z. diploperennis* (Figure 3) takes place through open, though directed, pollination. Because the plow is not used, the cultivated field requires hand weeding. This done with

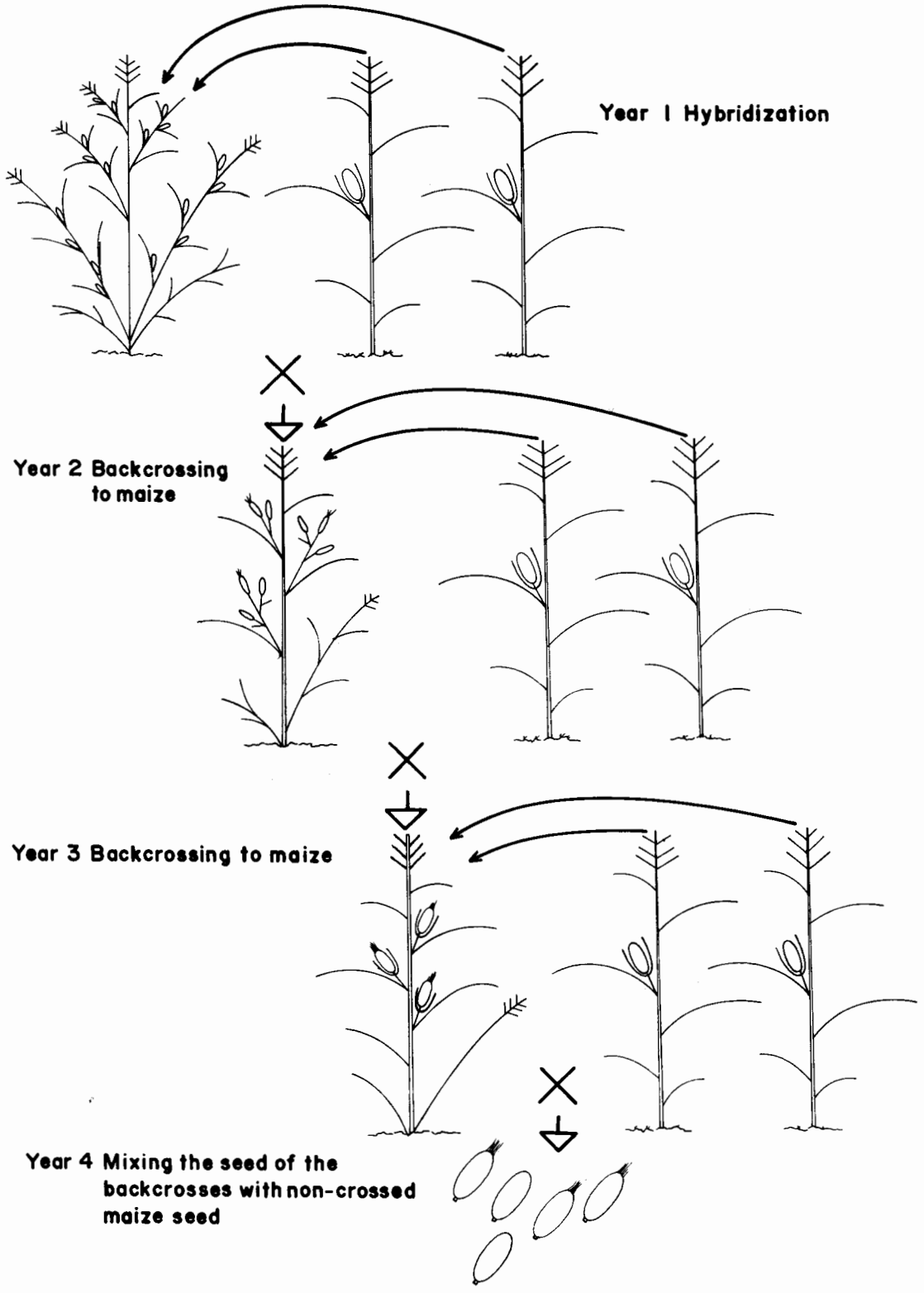


FIGURE 3 - Diagramatic representation of the hybridization, selection and incorporation of the germplasm between *Z. diploperennis* and maize (Race Reventador) carried out by the people of San Miguel. The process depicted takes only three generations whereas in some cases backcrossing and selection may take five years or more. The steps shown are, the initial hybridization, *Z. diploperennis* as the female parent, conducted at the end of the first year, two subsequent generations of backcrossing to maize, and the final mixing of this seed with the maize seed for the subsequent year's planting.

a machete at least twice a year to reduce competition from the 90 or more species of plants commonly occurring in the fields. During the first weeding a few of the tallest stems of *Z. diploperennis* are left standing among the maize plants. These few stems are far outnumbered by the number of maize plants thus are expected to receive a large percentage of maize pollen, this ultimately producing the hybrid seed. The seeds from these few stems of *Z. diploperennis* are gathered with the maize during harvest but saved seperately to be planted the following year. During the second year the hybrid seed is planted; usually in its own row to one side of the field. The plant develops normally, which is to say that it is not pruned as is the case in the preceding year. Here again the number of maize plants far exceedes the number of first generation hybrids, this leading to second generation backcrossed-seed with maize as the recurrent parent. The procedures in the third year follow, for the most part, those of the second year. It is following the third year that the people say that the milpilla has turned into maize. The architecture of the plant at this time certainly resembles more that of a maize plant than *Z. diploperennis* and it is at this stage that the people mix the seed of the second generation backcross with the seed of the maize that they will plant the following year.

According to the people of San Miguel, this process of turning "the milpilla into maize" increases production and confers resistance to at least two of the maize pests causing damage locally. According to one of the local residents, the process of hybridization and potential introgression may increase yield by a factor as much as one third (from 60 hectoliters to 80 hectoliters/hectare). Second, this process apparently makes the maize less suseptible to a fungal(?) disease known as *chahuistle,* a disease causing ear-rot and increasing susceptibility to cornborer. Finally, turning the milpilla into maize also results in a harder grain (this expected knowning that the grain of the local land race is a flint or floury while the seed of *Z. diploperennis* is very hard and crystaline) which resists damage by weevils and thus can be stored for a longer period of time.

Whether each of these characteristics are due to hybridization, introgression and selection is still conjectural and merits further study.[1] The increased yield seems rather incredible but while yields are locally rather low in general, and no fertilizer, insecticide, fungicide and little or no herbicide are used, such might be the case due perhaps to an increase prolificacy so notable in maize-teosinte hybrids and their use of volume to measure yield. Resistance to fungal pests seems unlikely. From what little we have seen in the field *Z. diploperennis* is affected by at least one of the fungal pests of maize (e.g., *Ustilago maydis),* though perhaps we are dealing with something other than fungal diseases (see Nault *et al.,* 1982). The greater resistance to grain storage pests seems quite likely, the seed of the first and later generation hybrids is quite dense, very likely poppable.

Discussion and Summary

The results presented above indicate that today *Z. diploperennis* is not a species of virgin forests. Its presence and persistence in human-manipulated habitats, and its indigenous association with locales that demonstrate ancient human occupation and environmental modification for agricultural purposes, point to a very long association with humans, possibly a dependence on them. While the milpilla now appears quite capable of maintaining itself in its human manipulated environments, this obviously does not indicate that it has always received the benefits from such a relationship. Whether its "original" habitat was an open pine-oak forest (GUZMAN 1982), we can be sure that natural disturbance would have been very important for *Z. diploperennis* until humans made their appearance.

The process of promoting hybridization between maize and the milpilla follows a practice widespread in Mexico where teosinte is common (WILKES 1970, 1972, 1977). We are presently unaware of attributes other than increased productivity, such as disease or insect resistance and longer storage life, being exploited in the hybrid and backcross generations of other species of teosinte under a system of traditional management as is here suggested for *Z. diploperennis.*

The older stands of the species show a tendency to produce taller stems and a greater number of female inflorescences, as well as a greater density of stems per square meter. We attribute the two former characteristics to increasing competition in the later stages of secondary succession. Decreasing species richness associated with longer abandonment time support this conclusion in a general way. We attribute greater stem density to increased production of ramets in the "relatively" late stages of secondary succession while the lower stem density noted in two stands (Las Playas - 5 years following abandonment; San Miguel Parcel 1 - under cultivation) we attribute to grazing, and the burning and pruning associated with cultivation.

In theory, *Z. diploperennis* should have relatively greater success maintaining itself through reproduction (by means of seed) in the early stages of secondary succession, and greater success by investing less in reproduction and more in growth (vegetative "reproduction") in the later stages. If this is indeed the case, then we are led to predict that the seed produced by the older-aged stands will show relatively less genetic diversity than that produced by younger-aged stands. The diminuitive size of the stands in Las Joyas in comparison to those in San Miguel, the larger size of the population in San Miguel, and the postulated longer span of human habitation in Las Joyas, all suggest that active management promises to maintain populations of the milpilla in a healthy state. The combination of large population size and emphasis on sexual reproduction under conditions of active management, such as seen in the valley of San Miguel, should maintain a higher level of genetic diversity than one might see in the Las Joyas population. This obviously warrants more attention if we are to confidently manage the species and assure its perpetuation. In the meantime, however, it would seem a shame to promote or even permit agricultural development of the existing traditional system until we are sure that the changes such development implies will not threaten the species in its natural habitat.

Endnotes

[1] While hybridization and introgression between maize and teosinte have been reported or hypothesized by many, thorough study of the evidence has shown that introgression of maize into the teosintes is probably nonexistent and that teosinte introgression into maize is rather slight (DOEBLEY 1984; DOEBLEY *et al.*, 1987). The existence of gene flow from maize to *Z. diploperennis* is doubted by KATO and LOPEZ (1990). While future investigations at the nuclear level will specifically seek to document the existence of introgression in both directions, it is also likely that introgression is occurring at the cytoplasmic level. Backcrossing to maize following hybrization using *Z. diploperennis* as the female parent should have, in a span of a few generations, created a miscegenation with a predominantly maize nuclear genome and cytoplasm of the milpilla.

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