

Population structure and ecology of a tropical rare rhizomatous species of teosinte *Zea diploperennis* (Gramineae)

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Abstract: One of the objectives of the Sierra de Manantlán Biosphere Reserve (Jalisco, México) is the conservation in situ of the teosinte *Zea diploperennis* Iltis, Doebley, Guzman & Pazzi. *Zea diploperennis* is perennial, shade intolerant and its 1-3 m shoots are architecturally similar to maize. Clonal growth is of the phalanx type. Genets are iteroparous (modules semelparous). The demography of seven module and genet populations was studied in seven sites representing three stages of old-field succession. Seven permanent one-meter-square plots were randomly established in each site. All genets initially present and those that became established during our study were mapped and labeled according to year of establishment. The magnitude of demographic fluctuations was greater in module populations. Genet population dynamics followed a seasonal rhythm with a maximum population size obtained at the onset of the rainy season. A relation was documented between percent annual mortality of a cohort and its age: the younger the cohort, the greater the mortality. This was a statistically significant relationship, $Y = [\sin(-0.288x + 1.657)]^2$ ($r = 0.92$, $p < 0.01$), where Y is proportion annual mortality of genets and x is the age of the cohort. The maximum rates of genet mortality occurred during the rainy season when population densities were greatest. As a consequence, we postulate that competition occurs principally during the rainy season. Linear relationships were observed between rate of population increase of genets versus old-field successional stage and soil type. Those areas with poor soil (Ultisol), degraded soil or soils with similar physical characteristics could be rehabilitated by introducing *Z. diploperennis*. Such rehabilitation would achieve two distinct objectives, promote propagation of this rare endemic and reclaim areas that are susceptible to

autoecology and natural history of rare species is one area in which ecologists can apply their experience to current problems in conservation biology or recovery plans (Harvey 1985, Brusard 1991, Boyce 1992, Huenneke 1995, Tear *et al.* 1995). However, to be successful, this outlook must be applied in long-term conservation programs. Demographic monitoring of rare plant species is an essential component of an effective species management program (Gilpin & Soulé 1986, Owen & Rosentreter 1992, Olmsted & Alvarez-Buylla 1995) in which active manipulations might be part of such a program (Boyce 1992).

One of the objectives of the Sierra de Manantlán Biosphere Reserve is the conservation in situ of the teosinte *Zea diploperennis* (Jardel 1992), a rare endemic species narrowly restricted in geographic range to a few hundred hectares (Rabinowitz *et al.* 1986). In spite of the fact that teosintes (wild *Zea* L. Gramineae) are a potential source of economically valuable germoplasm for maize's improvement (Iltis *et al.* 1979, Hoyt 1988, Sánchez-Velásquez 1991, Wilkes 1994), their basic population ecology has not been studied under local natural conditions. *Zea diploperennis* is a tropical endemic species occurring naturally in patches on approximately 360 hectares in the Sierra de Manantlán Biosphere Reserve in Jalisco, México (Benz *et al.* 1990). Growth and development appear to be favored by traditional forms of slash and burn agriculture (Sánchez-Velásquez *et al.* 1991). *Zea diploperennis* is a perennial, shade intolerant, rhizomatous grass whose one

implement a management program to conserve *Z. diploperennis* in situ. We describe the structure and population flux of genets and modules of seven populations of *Z. diploperennis*. We also evaluated the relationship between various environmental factors (altitude, exposure, slope, and soil type) and the stage of old field succession, and demographic attributes (rate of increase of genets and modules and genets arrival). In addition, we explored the relation between age and rate of mortality genet.

MATERIALS AND METHODS

The seven study sites are located in the Las Joyas Scientific Station in the Sierra de Manantlán Biosphere Reserve in Jalisco, México (19°36'N, 104°16'W). Grazing and forest fires have been excluded since 1988 from all sites. All sites are old abandoned maize fields; these are: Coamil 1 (Site 1), Coamil 2 (Site 2), Playas (Site 3), Huiscorol (Site 4), Zaramoro (Site 5), Asoleaderos (Site 6) and Asoleaderos del Tlacuache (Site 7), which represent three different time intervals since abandonment, i.e. different successional stages (Table 1). The characteristics of each site and its history are listed in Table 1.

Seven permanent one-meter square plots were randomly established in each of the seven abandoned fields. All genets present initially and those that became established subsequently were mapped and labeled according to the year of establishment (cf. Sarukhán & Har-

year-old cohorts were performed. The number of genets established by themselves, the total number of genets and modules (initial and final), and rate of increase of genets and modules, were compared according to successional stage and environmental factors (altitude, exposure, slope and soil type) using procedure two factors general linear model (GLM) with values previously transformed to ranks (except rate of increase of modules and genets) and *a posteriori*, multiple comparisons using Tukey's test from Statistic Analysis Systems

(SAS) version 6.03 (Seaman *et al.* 1994). In this case, performing analysis of variance (ANOVA) with values transformed to ranks is more conservative than the corresponding ANOVA without transformation and is frequently more accurate than the non parametric Kruskal-Wallis test (SAS 1988). In addition, we used a general linear model procedure to obtain the relationship between proportion annual mortality of genets (these values were previously transformed to their square root and then arcsine were calculated) and age cohorts.

TABLE 1

Characteristics of the Zea diploperennis study sites

	Site							
	1	2	3	4	5	6	7	
Altitude (m)	1960	1980	2000	2030	1960	1960	2020	
Exposure	SW	SW	SW	S	NW	S	S	
Slope (%)	10-20	10-20	0-5	10-20	10-20	10-20	10-20	
Soil type ^a	Alfisol	Alfisol	Ultisol	Alfisol	Alfisol	Ultisol	Ultisol	
Surrounding Vegetation	MMF PQ,SV	MMF P,SV	MMF P,SV	MMF P,SV	MMF P,SV	MMF P	MMF P	
Abandonment time (years)	4	4	4	14-17	14-17	17-19	17-19	

RESULTS

Population flux of genets was analyzed during two reproductive cycles from May (year one) to December (year two). The initial number of genets (May year one) did not differ significantly among successional stages ($F = 0.31$, $p \gg 0.05$), nor was there a significant difference among the final number of genets (December year two; $F = 3.2$, $p > 0.05$; Table 2). Furthermore, the difference in the recruitment between them was not significant during May year one and December year two ($F = 2.13$, $p > 0.05$; Table 2e). However, the oldest successional stage had higher rate of increase of genets than the other stages ($F = 4.65$, $p < 0.05$; Table 2d).

Similarly, we analyzed the module populations from December year one to December year two (final phase of two reproductive cycles). The percent age of survival of modules was zero because modules are semelparous. No difference was observed in the average number of modules by stage in December year one ($F = 0.01$, $p \gg 0.05$; Table 3a) nor in December year two ($F = 0.04$, $p \gg 0.05$; Table 3b). The annual rate of increase of modules was not significantly different ($F = 0.07$, $p \gg 0.05$) (Table 3d). The greatest number of modules was observed during the month of May year two in all stages, with stages 1 and 2 having the greatest overall number of modules (Table 3f).

The general pattern of genet densities was similar across all sites (see Fig. 1 two

two final). The highest genet mortality rates occurred from August to October and were greatest for cohorts were born in year one (Fig. 2a). When young genets initiated growth, more than 50 percent appeared chlorotic and died by damping-off. The remainder disappeared from areas excavated by gophers and due to unknown causes. Genets born before two or more years from initial study showed a greatest mortality from July to October in both years (Fig. 2a). Genets mortality appeared to be relatively more stable for all cohorts as time passed.

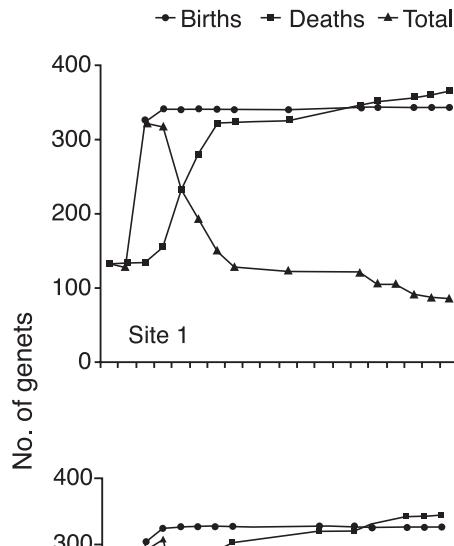


TABLE 2

Flux of Zea diploperennis genet populations in three different stages of old field succession

Stage age (yr):	4	14-17	17-19
(a) Mean No. of genets	21+3.4	19+3.5	21+3.4
No. of genets	25+2.8 ^a	22+4.2 ^a	27+4.2 ^a
May year one			
(b) Mean	23+3.5	26±6.3	40±5.4
No. of genets	22+2.6 ^a	22+4.2 ^a	33+3.7 ^a
December year two			
($X \pm S_{\bar{X}}$)			
(c) Net change	9	36	27
(all plots)			
(d) Rate	1.3±0.16 ^a	1.3±0.22 ^a	2.6±0.61 ^b
of increase			
(total No. of genets			
December year two/			
total No. of genets in			
May year one)			
(e) Mean	30±3.8	54±20.3	48±5.9
No. of Genets	22+2.5 ^a	24+4.7 ^a	31+3.6 ^a
($X \pm S_{\bar{X}}$)			
established between			
May year one and			
December year two			
(f) Total	680	796	649
No. of genets			
mortalities between			
May year one and			
December year two			
(g) Total no. of	278	153	183
genets present May			
year one alive by			
December year two			
(h) Percent	63	58.1	61.7
survival of genets			
(g/total number			
of genets) X 100			
(i) Expected	4.15	4.06	4.08

Patterns of module population fluctuations were similar for cohorts of the same age across sites. The number of modules from genets were born in year one was similar to genet survival curves of the same age probably because genets generally begin with a single module. The greatest number of modules was recorded during the months of July from year one and May from year two, and slowly decreased from August to November. The cohort born in year two contributed with a relatively lower number of genets and modules than the previous cohorts (Fig. 2b).

Genets born in year one and before were most abundant in sites one, two, three, four, five six and seven (Table 4). The most abundant cohorts at site three were genets of two and three year old. Recruitment during year two was zero at sites two, four and five, with the other sites showing very low recruitment. Proportion mortality (from May year one through December year two) among age cohorts was significantly different ($F = 123.4$, $p \ll 0.01$). The relationship between proportion of genets mortality and age was estimated as: $Y = \sin(-0.288X + 1.657)^2$, where Y is the proportion of mortality and X is the age of the cohort, was significant ($r = 0.92$, $p \ll 0.01$). Soil type explained significant differences in genets increase rate (Ultisol > Alfisol, 2.31 ± 0.4 and 1.2 ± 0.1 ; genets in December year two/genets in May year one respectively; $F=8.64$, $p < 0.01$).

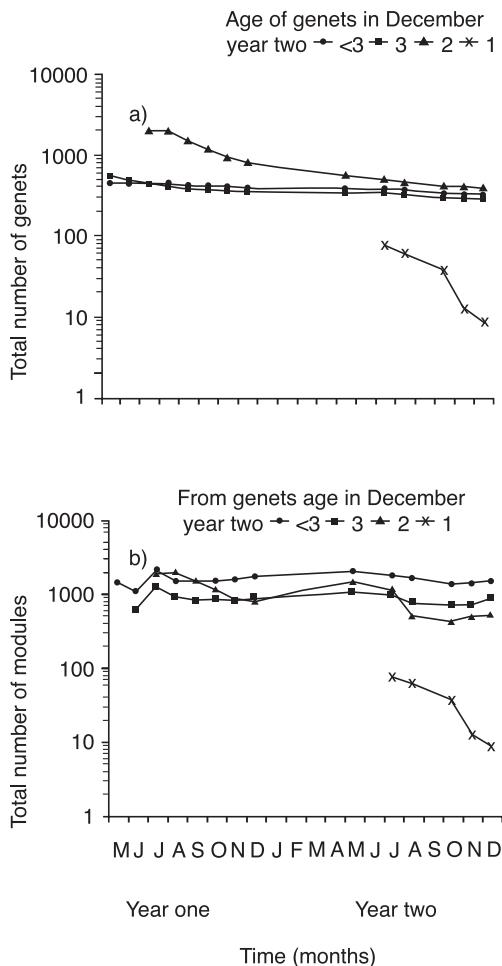


Fig. 2. a. Survival of genet cohorts of *Zea diploperennis*, total number of genets by age cohorts (1, 2, 3, and > 4 year-old in December year two) across site. b. Total number of modules as a function of date for *Zea diploperennis* born before two or more years from initial study, genets born

it is important to monitor genet flux for a greater length of time because there was high variation in density during both years. Thus appropriate models of population dynamics must be based on numerous years of monitoring in order to adequately conduct projection and population viability analysis.

No trends between the successional stage or environmental factors (altitude, exposure, slope and soil type) versus module population parameters were observed (Table 3). Our results differ from Benz *et al.* (1990) who worked with the same species yet demonstrated a significant positive relationship between number of modules and age stages. Perhaps their trend is a result of having included three sites in each of two localities differing in management history: three sites in San Miguel with very young stages and three others with old stages in Las Joyas.

In our study, the net change of modules was negative for all stages (Table 3c). The oldest stage had a smaller net change of modules. Perhaps this was a consequence of secondary vegetation absence encircling the sites. In this case, there is little potential for invasion by other rhizomatous species.

Module reproduction was synchronized across sites. The greatest number of modules in each site coincides with the month following the first month (June) of the year with precipitation, and the lowest number of modules was observed during the months with less precipitation (October-December). In all plants water availability appears to favor growth and

ley 1990), where older established individuals are competitively superior to their younger counterparts, as has been demonstrated for *Solidago canadensis* (Hartnett & Bazzaz 1985), *Fagus crenata* populations (Nakashizuka 1987 review of Crawley 1990) and *Bouteloua gracilis* populations (Aguilera & Lauenroth 1993). This pattern characterizes species where intraspecific competition appears to be responsible for the suppression of recruitment after the initial colonization (initial seedling recruitment, according to Eriksson (1993)).

As in the case of *Ranunculus acris* and *R. bulbosus* (Sarukhán & Harper 1973), the total number of genets per site in populations of *Z. diploperennis* exhibited a seasonal rhythm with peaks during spring time and was more evident in year two (Fig. 1, Fig. 2). The greatest genets mortality occurred during the season of greatest growth, i.e., the rainy seasons (July through September). This is similar to mortality patterns described for *R. canadensis* (Hartnett & Bazzaz 1985), *Lolium perenne* and other clonal grasses (Langer *et al.* 1964, Kays & Harper 1974). These patterns suggest that intraspecific competition may regulate genet mortality (Sarukhán & Harper 1973).

Growth active of rhizomatous perennial *Z. diploperennis* occurs immediately after the first rains following a dry season. As a consequence, we postulate that interspecific and intraspecific competition occurs principally during the rainy season, which coincides with the period when the maximum rates of genet mortality occur. Our results concur with the hypothesis offered

The degradation of soils in the Sierra de Manantlán Biosphere Reserve is caused primarily by forest fires, slash and burn agriculture and cattle grazing (Pineda 1988, Jardel 1991, Sánchez-Velásquez & García-Moya 1993, Sánchez-Velásquez *et al.* 1996, Hernández 1998). Those areas with poor soil (Ul-

tisol) or soils with similar physical characteristics could be rehabilitated by introducing *Z. diploperennis*. Such rehabilitation would achieve two distinct objectives, promote propagation of this rare endemic and reclaim areas that are susceptible to erosion and further degradation.

TABLE 3

Flux of Zea diploperennis module populations in three different stages of old field succession

Stage age (yr):	4	14-17	17-19
(a) Mean No. of modules ($\bar{X} \pm S_{\bar{X}}$) December year one	72±9.8 25±2.3 ^a	70±13.2 25±4.3a	64±8.9 25±3.8 ^a
(b) Mean No. of modules ($\bar{X} \pm S_{\bar{X}}$) December year two	64±10.4 25±3.3 ^a	54±8.2 24±3.5 ^a	61±11 25±4.1 ^a
(c) Net change (all plots)	-168	-224	-42
(d) Rate of increase (total in year two/ total in year one)	0.89±0.1 ^a	0.94±0.12 ^a	0.9±1 ^a
(e) Expected time for complete turnover (yr) ((1.42/100-h*) X 100)	1.42	1.42	1.42
(f) Maximum no. of modules	1717	1273	1089

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RESUMEN

Se estudió la demografía de *Zea diploperennis* en siete sitios de cultivo abandonados. La magnitud de las fluctuaciones demográficas fue más grande en las poblaciones de módulos. La dinámica de las poblaciones de genets siguió un ritmo estacional con un tamaño máximo de la población al inicio de la temporada de lluvias; las cohortes más jóvenes presentan la más alta mortalidad, *i. e.*, $Y = [\sin(-0.288x + 1.657)]^2$, ($r = 0.92$, $p < 0.01$), donde Y es la proporción de la mortalidad anual y x es la edad de la cohorte. La máxima tasa de mortalidad de genets ocurrió durante la temporada de lluvias cuando la densidad de la población fue más alta, cuando la competencia parece mayor. Hubo relaciones lineales entre la tasa de incremento de genets y el estado sucesional y el tipo de suelo. Aquellas áreas con suelos pobres degradados o suelos con similares características, pueden ser rehabilitados introduciendo *Z. diploperennis*, protegiéndola y combatiendo la degradación del suelo.

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