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Population dynamics of *Zea diploperennis*, an endangered perennial herb: effect of slash and burn practice

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Summary

1 *Zea diploperennis* is a wild relative of maize that is endemic to the Sierra de Manantlán Biosphere Reserve in Mexico. Because this species is a priority for conservation in the reserve, the effects on its populations of the most common types of anthropogenic disturbance – slash-and-burn, and slash without subsequent burning – were investigated in three populations for 5 years.

2 The patterns of establishment and mortality were similar in all populations studied. Numbers of ears and fruits produced were significantly higher when disturbances were applied.

3 Because permanence is the most important stage in contributing to λ, the results suggest that the first genets to become established have an advantage over newly recruited plants.

4 When the two disturbance types were applied, λ was close to 1 or > 1. After the first disturbance, λ increased by almost 100%. In almost all situations, with or without disturbance, the persistence loops of *Z. diploperennis* are the most important life history pathways in the relative contribution to λ. In general, when λ increases, sexual growth loops also increase in importance, and persistence loops decrease. Changes in λ are not related to changes in vegetative growth loops.

5 If populations of *Z. diploperennis* are not disturbed at least once every 5 years, then species will go locally extinct in the wild.

Key-words: demography, disturbances, loop analysis, teosinte, *Zea diploperennis*

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Introduction

The study of population regulation and demography in natural habitats is extremely important for the conservation of rare and endangered species and for the sustainable management of economically important species (Harvey 1985; Brussard 1991; Owen & Rosentreter 1992; Olmsted & Álvarez-Buylla 1995; Oostermeijer *et al.* 1996; Lesica 1999; Caswell 2000; Menges 2000; Kaye *et al.* 2001). Although *teosintes*

– the wild relatives of maize – have a large economic potential for the improvement of cultivated maize (Wellhausen *et al.* 1951; Sánchez & Ordaz 1987; Iltis 1993), they have received little attention from the ecological point of view and no demographic studies have involved *in situ* monitoring (Sánchez-Velásquez 1991). The *teosintes* are associated with anthropogenic disturbances, and great importance has been ascribed to their possible influence on the formation and variability of the main varieties of maize in Mexico, as their reproductive system allows for natural hybrids and genetic flow between wild and cultivated plants (Wellhausen *et al.* 1951; Sánchez & Ordaz 1987; Iltis 1993). *Zea diploperennis* Iltis, Doebley, Guzmán and Pazy, the most recently described perennial species of

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teosinte (Iltis *et al.* 1979), is restricted to the Sierra de Manantlán Biosphere Reserve in Jalisco, Mexico. The interest in its conservation derives from its very narrow geographical range, although it is locally abundant, with crowded populations in discrete patches. Indeed, one of the objectives of the Sierra de Manantlán Biosphere Reserve and the associated Manantlán Institute (University of Guadalajara) is the *in situ* conservation of this *teosinte* (SEMARNAP 2000).

Small-scale fires occur every year in Manantlán, mostly as a result of uncontrolled burning from the *coamil* agricultural system (a slash-and-burn land management technique used locally). Disturbances are also created by cattle grazing on natural vegetation. It has been shown that, in experimental mixed cultivation with maize, the growth of individual plants of *Zea diploperennis* is favoured by these disturbances (Sánchez-Velásquez *et al.* 1992). However, the effect of disturbances has not been evaluated at the population level.

The Las Joyas Field Station, within the core area of the reserve, is close to large populations of *Zea diploperennis* (Benz *et al.* 1990). These populations have been protected from grazing and forest fires since 1988, as part of management policies aimed at protecting the core area of the reserve and conserving populations of *Z. diploperennis* (Jardel 1992). No new agricultural areas have been opened in Las Joyas since that date (Lorente-Adame & Sánchez-Velásquez 1996). Management options are urgently needed to make the protection of *teosinte* compatible with other conservation activities within the reserve.

Our objective was to analyse and compare the effects of two types of anthropogenic disturbance (slash-and-burn vs. slash-without-burning) on the demography of *Z. diploperennis*. In particular we aimed: (a) to describe population changes during 5 years in plots under different disturbance regimes; (b) to assess the relative contribution of different life-history stages to population growth under different sequences of disturbance; and (c) to identify disturbance regimes that may promote the persistence of populations of *Z. diploperennis*.

Materials and methods

SPECIES AND STUDY AREA

Zea diploperennis (Poaceae) is a heliophyllous, rhizomatous species of *teosinte*, with semelparous annual aerial stems (ramets) that branch from a perennial iteroparous genet. The shoots are similar in appearance to those of maize and around 2 m high (Sánchez-Velásquez 1991). Clonal growth is 'phalanx-type' (Hutchings & Bradbury 1986), developing radially from the parental shoot with short rhizomes that form a compact circular front. The plants can grow in association with maize fields under traditional *coamil* cultivation (Benz *et al.* 1990; Sánchez-Velásquez *et al.* 1992). *Zea diploperennis* is dispersed into newly slashed

plots by cattle and sometimes also by farmers who promote its growth as a source of forage for their livestock and of hybrid vigour for their maize crops. Iltis *et al.* (1979) and Benz *et al.* (1990) have described the taxonomy and general biology of the species. The potential of *Z. diploperennis* as a source of genes for maize breeding is internationally recognized (FAO 1989).

The Sierra de Manantlán is located in Southern Jalisco, Mexico. It comprises oak forests in the lower elevations, and pine and montane mixed forests in the higher ranges. The sites where *Zea diploperennis* is found are within montane forest habitats at altitudes ranging from 1900 to 2100 m and located at approximately 19°36'?N and 104°16'?W. Mean annual temperature in these sites is *c.* 16 °C and mean annual precipitation is around 1700 mm (Hernández *et al.* 2000). A dry period occurs from February to May and a wet period from June to October. Occasional winter rains, derived mostly from tropical hurricanes forming in the Pacific coast of Mexico, may fall between November and January (Martínez *et al.* 1991).

PERMANENT PLOTS AND EXPERIMENTAL TREATMENTS

We studied three populations in three similar areas within Las Joyas from 1988 to 1993. All sites are less than 1 km apart. All are old maize fields that were abandoned from agriculture in the mid-1970s. Seven permanent 1 m² plots were randomly established in each of the sites. All genets initially present, and those that became established during our study, were mapped and labelled according to year of establishment. In May 1989 we could differentiate the genets that were recruited in 1988 because they had one or rarely two small shoots, and no ears or only one ear. Cohorts of plants recruited from seed during the 5-year study period were identified by means of the plot map from the previous year, and also by their leaf apex. The first two leaves in a true seedling have an emarginate apex, but later leaves, or new leaves from vegetative shoots, have an acuminate apex. Dead plants were identified by the absence of green shoots and buds, and/ or by their disappearance from previous locations. In the first 3 years, we mapped the plots from May to December at intervals of approximately 1 month. The number of shoots per genet and the number of ears per shoot were counted during the months in which mature fruits were present. Because of the low frequencies encountered in some of the 1 m² plots, we combined the counts from each plot at each observation date to obtain a value for the whole site at that time.

In May 1991 we slashed all the secondary vegetation (woody scrub with dominant leguminous shrubs) from sites 2 and 3, without burning the stubble. In May 1993 we re-applied the same treatment to site 2, while in site 3 we used slash-and-burn (only burning inside the study site, ensuring that fire would not spread to the

surrounding forest). No disturbance was applied to site 1. Because of the rarity of the study species, the small size of the existing patches, and the scale of the disturbance treatments, it was not possible to apply all three treatments to all sites (it is especially difficult to apply fire safely during the dry season to only part of a site). We could not obtain authorization to apply fire in site 3 in 1991.

In spite of the lack of adequate replication, the three sites at Las Joyas have some important features that made them appropriate for this study. First, their management history is comparable, as they were abandoned from cultivation between 1970 and 1974. Secondly, as they are located within the core area of the reserve, they are amenable to controlled experimental treatments without conflicting with land use decisions made by farmers. Because of the extreme rarity of the study species, the sites we used were the only suitable sites for this study. Lastly, when setting up this experiment we were interested in evaluating the success of management in the core area of Manantlán for the conservation of *Z. diploperennis*. Thus, the three sites should be regarded as plots with contrasting management, and not as true replicates of an experimental treatment.

The permanent seed pool was estimated in 1990. At each site we took five random soil samples, 30×30 cm wide $\times 15$ cm deep in January 1990, immediately after seed production. We then took five additional samples in November 1990, after the annual rainy season and before the following seed production event. Seed pool was estimated as $P_{seed} = \dfrac{N_{Nov}}{N_{Jan}} \times 100$, where N_{Jan} is the number of viable seeds found in January (after seed production and before the rains), N_{Nov} is the number of viable seeds found in November (after germination during the summer rains, and before the dispersal of the new seed), and P_{seed} is the percentage of the seeds that did not germinate but remained viable in the seed pool (Lorente-Adame & Sánchez-Velásquez 1996). These percentages were later used in transition matrices for the simulation models.

PRODUCTION OF EARS AND CARYOPSES

To analyse the effects of disturbance and year on the production of ears for each genetic individual, we randomly selected 40 individuals from each site in each year. Through a Montecarlo process we calculated, for each year, 1000 differences in the number of vegetative shoots between pairs of randomly selected individuals between two sites (without replacement). By analysing the differences between sites through time, we removed the fixed effects of the sites and focused on the site × year interaction. Thus, if the distribution of differences in the number of ears from one year to the next remained the same, we can conclude that plants from both sites produced ears at the same rate as in the previous year. On the other hand, if the distribution produced by the Montecarlo simulation changed
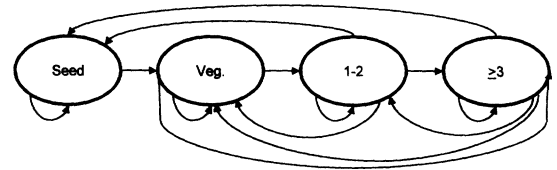
Fig. 1 The life cycle graph for *Zea diploperennis* genets: s = seed; veg = genet, without flowering shoots; 1–2 = genet with 1–2 flowering shoots; ≥ 3 = genet with 3 or more flowering shoots.

significantly between years (shown by a *t*-test), we can conclude that the relative number of ears produced in one site had increased or decreased significantly compared with the other site. The significance threshold for the *t*-test was subjected to a Bonferroni correction to allow for multiple non-independent tests.

In December 1993 we collected 53 ears at random from each site. In the laboratory, we counted the number of seeds (caryopses) in each ear and then transformed these values to ranks (SAS 1988). We then analysed the transformed results for between-site differences, followed by a SNK multiple-comparison test (Seaman *et al.* 1994).

PROJECTION MATRIX MODELS

At each site and for each year, we calculated Markovian transition probabilities for the genets, dividing their life cycle into four stages: (a) seeds; (b) genets without flowering shoots; (c) genets with one to two flowering shoots; and (d) genets with three or more flowering shoots (Fig. 1). The population growth rate (λ, the dominant eigenvalue of the transition matrix), the stable-size class distribution, and the elasticity values for each of the 12 matrices were calculated by iterative matrix multiplication. To eliminate the fixed effect of sites, we subtracted for each λ-value in each site the value of λ for the year 1989, during which none of the sites had been subject to the disturbance treatments. Thus, for each site we transformed the series of four yearly growth rates (in which the fixed effect of site may bias our statistical analysis) into a new series of three deviations from the value in 1989 (from which the fixed effect of the site had been removed). Inter-site comparisons were made on the transformed series.

Loop analysis

An appropriate method for comparing the relative contributions of different life-history stages to the population growth rate is demographic loop analysis (van Groenendael *et al.* 1994; Wardle 1998; De Kroon *et al.* 2000). The method, as applied in this study, consisted of four basic steps, as described by Wardle (1998): (i) We constructed a life-cycle graph and population transition matrix for *Z. diploperennis*. (ii) We calculated the elasticity values of the matrix. (iii) We decomposed the life cycle graph into unbranched loops

in such a way that all transitions were incorporated at least once into a loop. The characteristic elasticity of the loop was estimated as the elasticity of the transition element that is unique to the loop. (iv) The loop elasticity was calculated by multiplying the characteristic elasticity by the number of transition elements within the loop. The software developed by van Groenendael *et al.* (1994) was used.

The analyses were made using a program based on the theory of loop analysis (van Groenendael *et al.* 1994). The final output of the program is the relative contribution of each loop to the population growth rate λ. We classified all the possible loops in the *Z. diploperennis* transition matrix into three different categories: (a) persistence loops, i.e. loops in which a given category at time *t* remains in the same category at time *t* + 1; (b) sexual reproduction loops, i.e. loops that involve the category of seed in the loop; and (c) vegetative loops, i.e. loops that generate new categories without going through the seed stage. Finally, by summing all the relative contributions of each set of loops to λ, we could estimate the contributions of persistence, sexual reproduction and vegetative growth to population dynamics.

Simulation analyses

One widely used method for exploring the consequences of different management scenarios is to project the population transition matrices following predefined rules (Caswell 1989; Ehrlén & van Groenendael 1997; Tuljapurkar & Caswell 1997). These population dynamics simulations help in understanding how different management decisions could affect the protection of rare species. Our goal was to determine how frequently disturbance must be applied if it is going to be beneficial to *Zea diploperennis* populations. We used four transition matrices to simulate different management scenarios for each population in each site: the 1989–90 matrix corresponds to an undisturbed situation in all three sites, the 1990–91 matrix corresponds to a disturbed situation (slash) in sites 2 and 3, the 1991–92 matrix corresponds again to an undisturbed situation in all sites (although sites 2 and 3 were recovering from previous disturbance), and the 1992–93 matrix corresponds again to a disturbed situation (slash in site 2 and slash-and-burn in site 3).

By applying the 1989–90 matrix to the population vectors from each site we could project an 'undisturbed' situation, in which we used the 1990–91 matrix to project the demographic effects of disturbance. We defined for each site a series of six scenarios with growing frequency of disturbance. We constructed a 1/10 scenario, in which the 'disturbed' matrix was applied every tenth year to the demographic projections, a 1/7 scenario with disturbance every seventh year, a 1/5 scenario, a 1/3, a 1/2, and a 1/1 scenario in which the disturbance matrix was used for every projected year. A second set of analyses was done using the 1991–92 matrix to simulate years in which no disturbance

was applied, and the 1992–93 matrix to simulate experimental disturbance. In the case of site 1 (without disturbance), the same simulation years were used.

Results

SEED POOL

The proportion of seeds that did not germinate between January and November 1990 but remained viable in the seed pool was 40% in site 1, 32% in site 2 and 34% in site 3. These values were used in the projection matrices. To simulate no disturbance, we used a probability of permanence of seeds in the seed pool of 0.4 (the value from site 1). To simulate slash disturbance, we used a probability value of 0.33 for seed permanence (the mean value from sites 2 and 3).

POPULATION DYNAMICS

Two periods of high recruitment were observed during the springs of 1989 and 1991, followed by two periods of high mortality in the summer and autumn of the same 2 years. In the other years (1990, 1992 and 1993) the peak of spring recruitment was much lower, or even undetectable, and the peak of summer deaths was also negligible. Superimposed on that seasonal cycle there was a general and sustained decrease in the number of genets. In all three sites the number of genets at the end of the observation period (November 1993) was lower than the number at the beginning (May 1989).

All later cohorts (from 1990 to 1993) consisted of too few established individuals to make any statistical tests on their mortality rates, and all plants in these cohorts died within periods ranging from 1 to 6 months. These results were confirmed by a step-wise multiple regression model for the pooled survival rates, including the effects of time, site and cohort. Significant differences were found between cohorts ($F = 18.06$; d.f. $= 3294$; $P < 0.01$) and a significant interaction term was also found between time and cohorts ($F = 9.65$; d.f. $= 3294$; $P < 0.01$), but no significant differences were attributable to the effect of either the site or the type of disturbance ($P > 0.05$).

The age-structure of the genets at the end of each growth cycle (i.e. October–November) for years 1–5 was similar in the three sites. The pre-1988 cohort was proportionally more abundant than other cohorts at the end of the study (November 1993) in all sites.

PRODUCTION OF EARS AND CARYOPSES

The Montecarlo simulation of production of ears between sites, showed no difference between 1989 and 1990 ($P > 0.05$). During these 2 years the effects determining fixed differences between sites remained relatively constant. In years 1991 and 1993, however, the distribution of intersite differences changed significantly in production of ears ($P < 0.05$) (sites 3 and 2 had higher number of ears). These years correspond to the
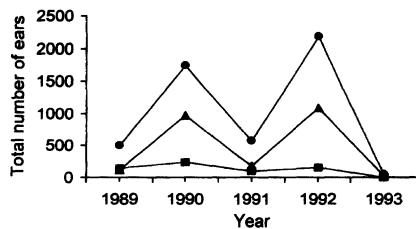
Fig. 2 Production of ears by *Zea diploperennis* in each year at the three study sites (squares, site 1; triangles, site 2; circles, site 3).

Table 1 Population growth rate (λ) of three *Zea diploperennis* populations from Sierra de Manantlán Biosphere Reserve, Mexico

Cycle year	λ Site 1 ($s1$)	Site 2 ($s2$)	Site 3 ($s3$)
1980–90	0.555	0.572	0.498
1990–91	0.734	1.108	0.868
1991–92	0.831	0.912	0.989
1992–93	0.855	1.100	1.069

Using the first year from each site as a control, $s1$ vs. $s2$ ($P = 0.04$), $s1$ vs. $s3$ ($P = 0.03$) and $s2$ vs. $s3$ ($P = 0.92$). Using first year from site 1 as a control, $s1$ vs. $s2$ ($P = 0.02$), $s1$ vs. $s3$ ($P = 0.01$) and $s2$ vs. $s3$ ($P = 0.99$).

dates of the experimental disturbances. Finally, in year 1992, sites 1 and 2 did not show significant differences ($P > 0.05$), but there were differences between site 3 and sites 1 and 2 ($P < 0.05$). The results suggest that the disturbance treatments had a significant effect on the production of ears and consequently on production of caryopses, independently of the fixed effects that may be ascribed to each site (Fig. 2). Additionally, the results suggest that in site 3 the increased fertility caused by disturbance in 1991 spilled over into year 1992.

Disturbance seemed especially to enhance the reproductive performance of the younger cohorts, as indicated by a highly significant interaction term between cohort and sites ($G = 409.9$; d.f. $= 2$; $P < 0.01$).

Significant differences were observed in the number of caryopses produced per ear between sites ($F = 3.99$; d.f. $= 2155$; $P = 0.02$). Reproductive shoots at site 1 produced significantly fewer caryopses per ear (6.35 ± 0.16) than those at sites 2 and 3 (7.08 ± 0.22 and 6.92 ± 0.19, respectively), which in turn did not differ significantly in caryopsis production.

PROJECTION MATRIX MODELS

The population growth rates of the genets were less than unity in all three sites at the beginning of the observations (1989; Table 1). After the first year, however, when the disturbance treatments were applied, the values of λ increased substantially in the disturbed sites 2 and 3, but less in the undisturbed site 1. When the series of λ-values was transformed into deviations from the base year (1989), it was found
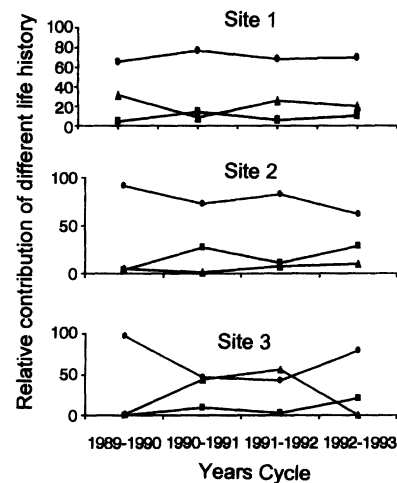
Fig. 3 Loop analysis in three populations of *Zea diploperennis*. The calculation of the relative contribution of alternative life history loops to fitness is based on the elasticity of the transition elements of the projection matrices (van Groenendael *et al.* 1994) (circles, persistence; squares, sexual growth; triangles, vegetative growth loops).

that the vector of residuals for site 1 was significantly lower than the corresponding vectors for sites 2 and 3 ($P < 0.04$ for both comparisons). The residual growth rates did not differ significantly between sites 2 and 3 ($P > 0.9$). That is, population growth rates tended to increase in sites 2 and 3, but did not increase similarly in site 1. It is also noticeable that in site 2, λ achieved values higher than unity in the 2 years in which perturbation was applied (1990–91 and 1992–93), and in site 3, λ was higher than unity after slash-and-burn was applied (1992–93). In site 1, in contrast, genet growth rates were always less than unity (Table 1).

Loop analysis

We found that the relative contribution of the three alternative life history pathways of *Zea diploperennis* – persistence, sexual reproduction and vegetative growth – varied between sites and years (Fig. 3). In years with disturbance, the contributions of sexual reproduction loops were relatively high. In contrast, the undisturbed site 1 showed consistently high contributions of the persistence loops to the plant's demography, and low contribution of sexual reproduction. By pooling all the 12 loop analyses together, it was found that a marked and significant ($P = 0.003$) correlation exists between the relative contribution of sexual reproduction and population growth (Fig. 4). Additionally, it was found that the mean elasticity of the sexual reproduction loops was significantly lower than that for the persistence and vegetative growth loops ($\bar{x} = 5.8 \pm 4.3$, 28.4 ± 6.5 and 8.2 ± 7.1, respectively).

Simulation analysis

The projection of population transition probabilities for the genets in site 1 (undisturbed) showed that,
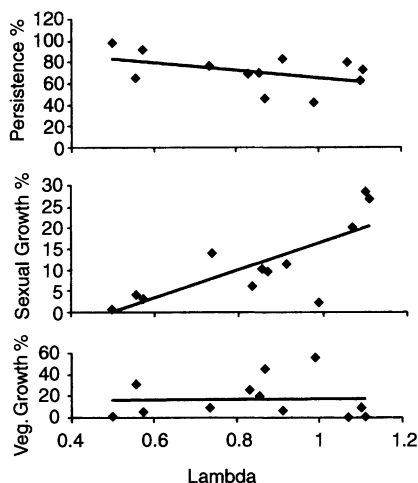
Fig. 4 Relationships between population growth rate (λ) and (a) persistence, (b) sexual growth and (c) vegetative growth loops. The persistence loops and the vegetative growth loops were not significantly correlated with λ ($r = 0.46$ and 0.03, $P = 0.13$ and 0.93, respectively), but the sexual growth loops were significantly correlated with population growth ($r = 0.77$, $P < 0.01$).

independently of the year that was used to calculate the matrix, the population of genets in this site would constantly decrease to local extinction (Fig. 5). The final fate predicted by the simulation of the populations in the other two (experimentally disturbed) sites depends strongly on the frequency and type of disturbance. In site 2, the simulation predicts that genets will increase in number if disturbance is applied at least once every 2 years (simulation with transition data from years 1989–90 and 1990–91), or once every 3 years (simulation with transition data from years 1991–92 and 1992–93); if the disturbance is applied each year, the number of genets increases exponentially with any transition data

(Fig. 5). In site 3, the simulation with transition data from years 1989–90 and 1990–91 failed to predict a net increase in the number of genets, although it clearly shows that genet extinction increases as disturbance frequency decreases. When data from years 1991–92 and 1992–93 were applied to site 3, the simulation predicts that genets will increase in number if disturbance is applied every year, and that biennial disturbances should be sufficient to maintain a large number of genets in the population for a considerable time (Fig. 5).

Discussion

EXPERIMENTAL TREATMENTS

Disturbances such as slash and burn have important effects on plant population dynamics (Loucks *et al.* 1985; Silva *et al.* 1991; Joy 1992; Whelan 1995; Kaye *et al.* 2001). Few of these studies, however, have been done on species of extreme rarity such as *Zea diploperennis*. Rare species with extremely patchy distributions, such as this one, constrain experimental work as proper replication cannot easily be achieved. In spite of this, the challenges imposed by extremely rare and endangered species must be met if their conservation is to be assured. This is especially true in the case of *Z. diploperennis* because of its obvious importance as a wild relative of maize. Taking advantage of the time series present in our data, and of the fact that during the base year (1989) all three sites had been subject to similar management, we eliminated the fixed effect of site from our statistical analyses whenever possible by subtracting the base year from the data series. By working with time differences, we have also reduced the pseudoreplication effect of repeated measures (Mead 1990).
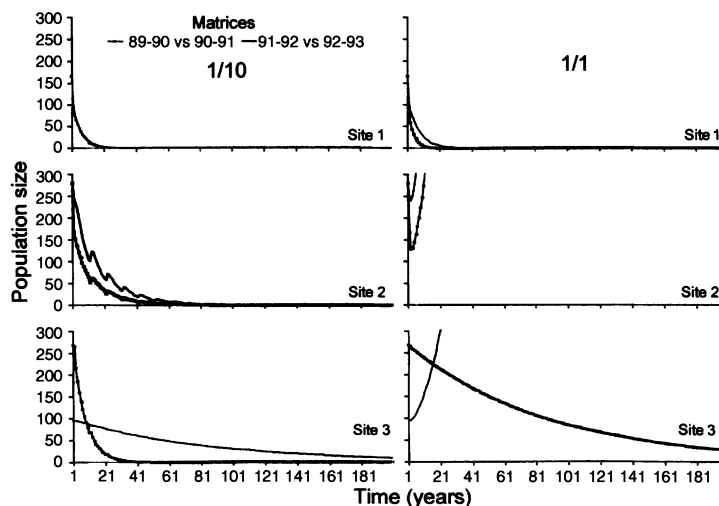
Fig. 5 Simulation analysis in three *Zea diploperennis* populations, showing simulated population sizes vs. time. Only two frequencies are exhibited. The ratio in the graph indicates the frequency of simulated disturbances (e.g. 1/10 indicates one simulated disturbance every 10 years). The dotted lines indicate simulations projecting the 1989–90 transition probabilities as the undisturbed condition, and the 1990–91 matrix as the disturbed condition. The continuous lines indicate simulations using the 1991–92 matrix for the undisturbed condition, and the 1992–93 matrix for the disturbed condition.

GENETS STRUCTURE

The age structures of the three populations of *Z. diploperennis* were dominated by three classes (pre-1988, 1988 and 1989 cohorts). It has been reported that in many plant species successfully established adults can obstruct the establishment of seedlings (Crawley 1990; Eriksson 1993), and that the presence of adults does not necessarily mean that the site is favourable for seedlings (Kays & Harper 1974; Lovett-Doust 1981; Eriksson 1988, 1993; Maddox *et al.* 1989; Aguilera & Lauenroth 1993; Sánchez-Velásquez 2001). It is not rare to find populations of clonal plants consisting of only one or two age classes (Crawley 1990; Higgins *et al.* 2000). It is also known that compact, 'phalanx-type' clonal growth, as observed in *Z. diploperennis*, promotes genetic homogeneity in space (Harper 1985; Hutchings & Bradbury 1986).

SEED POOL AND PRODUCTION OF CARYOPSES

Massive production of *Z. diploperennis* seeds was observed in our sites after disturbance, especially after burning. For fire-tolerant species, fires may help to eliminate potential competitors (Hughes *et al.* 1991; Watson *et al.* 1994; Howe 1995) and may also favour population permanence and growth (Silva *et al.* 1991; Gross *et al.* 1998). For centuries fire has been an important management tool for indigenous farmers in Manantlán, and has hence been an important element in the past demography of *Z. diploperennis* (Benz *et al.* 1990), while cattle have been one of the main dispersal agents of the plant's propagules (Benz *et al.* 1990; Guzmán & Iltis 1991). *Z. diploperennis* seems to be highly tolerant to these disturbances.

PROJECTION MATRIX MODELS

In the absence of disturbance, population growth of *Z. diploperennis* tends to be negative ($\lambda < 1$). Experimental disturbance produced a significant increase in the growth rates of the genets. Although slashing of the successional scrub produced an increase in the values of λ, this increase was especially high in site 3 after the combined application of slash-and-burn. In short, the disturbance brought about by slashing the scrub, or by slashing-and-burning, was sufficient to change the population growth rate from negative to positive. Silva *et al.* (1991) and Kaye *et al.* (2001) found similar dramatic increases in the population growth rates of the grass *Andropogon semiberbis*, and of *Lomatium bradshawii*, when burning was applied. Similar results have been found by other researchers, e.g. see Kaye *et al.* (2001).

Loop analysis showed that in almost all situations, with or without disturbance, persistence is the most important life-history pathway of *Z. diploperennis* in contributing to fitness (Fig. 3). Although, quantitatively, sexual growth loops contribute less to the species' fitness, bouts of seed production and subsequent

germination are the major causes of population increase. This was re-affirmed by the simulation studies, which show that only when disturbances are applied frequently (once every 2–4 years) does the growth of the population become positive.

FIRE AND CONSERVATION OF *ZEA DIPLOPERENNIS*

Fire is an important factor in the evolution and maintenance of many plant species, especially in fire-prone grasslands (West 1993; Whelan 1995; Menges & Dolan 1998) and conifer forests (Cottam 1981; Heinselman 1981). The effect of fires on a given population depends on the frequency and intensity of burning (White 1979; Pickett & White 1985). The growth of herb species can be positively affected by fire (Joy 1992; Oostermeijer *et al.* 1996; Lesica 1999; Kaye *et al.* 2001). The fact that the demography of genets in *Z. diploperennis* is not affected by disturbance, and that the production of ears is strongly enhanced by slash-and-burn management suggests that this species is adapted to disturbance in general, and to fires in particular.

The application of prescribed burning in *Z. diploperennis* populations at the Las Joyas Field Station is risky, as the high flammability of the dry stems of wild *teosinte* could cause the fire to escape into the adjacent forests. For this reason, we could not use a fire treatment in site 3 during the extremely dry season of 1991. Fires have been a disturbance factor in Manantlán for many years, adversely affecting the montane forests (SEMARNAP 2000). Our study suggests that the use of slash without burn has similar effects to those of slash-and-burn for individuals and populations of *Z. diploperennis*. Thus, simple slashing could be the most suitable management factor to maintain the populations of this *teosinte*.

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