# UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

## FACULTAD DE CIENCIAS

### DIVISIÓN DE ESTUDIOS DE POSGRADO

# EFECTO DE LAS PERTURBACIONES SOBRE LA DEMOGRAFÍA DE *Zea diploperennis*

# T E S I S

QUE PARA OBTENER EL GRADO ACADÉMICO DE

## DOCTOR EN CIENCIAS

## (BIOLOGÍA)

## P R E S E N T A

## LÁZARO RAFAEL SÁNCHEZ VELÁSQUEZ

291421

DIRECTOR DE TESIS: DR. EXEQUIEL MARÍA EZCURRA REAL DE AZÚA

Esta tesis fue dirigida por el siguiente comité tutorial:


Dr. Exequiel M. Ezcurra Real de Azúa, Tutor.
Dra. Elena Álvarez-Buylla, Asesor.
Dr. Miguel Martínez Ramos, Asesor.

# CONTENIDO

Dedicatoria

Agradecimientos

Reflexión y despedida

# DEDICATORIA

Le dedico esta tesis con todo mi amor a lo que mejor he hecho en mi vida, a mis hijas Frida Inés y Lorena. Estoy muy orgulloso de ustedes, por sus valores, criterio, honestidad, espíritu de lucha y su amor. Recuerden: "Por siempre las amaré, por siempre las querré, mientras en mi haya vida, siempre serán mis bebés".

A mi compañera de muchos años, con quien he compartido días de tristeza, alegría, y meditación. A diferencia de los poetas, considero que aún no existen las palabras ni los versos mas bellos del mundo para expresar mis sentimientos y decirte lo tanto que te quiero.

A mi madre, por haberme inculcado el respeto a la vida y el amor a las plantas. A la memoria de mi padre por haberme enseñado los tres principios básicos que me han ayudado en la vida.

A mis hermanos, Arturo, Joel, David, Pompeyo e Israel, quienes me brindaron su apoyo para que dentro de la familia hubiera, al menos, un profesionista, espero haberles cumplido. Con mucho cariño dedico esta tesis a mis sobrinos.

A todas aquellas personas que me han ofrecido su amistad sincera desde Coatepec Ver., en el barrio de la plaza donde pasé mi niñez, la colonia El Hongo en donde pase mi niñez - adolescencia, a la ciudad de Cárdenas Tabasco donde pase mi adolescencia, a las ciudades de Xalapa Ver., Texcoco Mex., El Grullo y Autlán, Jal., donde he pasado mi etapa de adulto.

A mis amigos y compañeros del Instituto Manantlán de Ecología y Conservación de la Biodiversidad, de una manera especial a: Luis Manuel, Ángela, Minerva, Sergio, Tania, Alfredo, Sagrario y Fernando. De una manera muy especial a mis amigos y a mis estudiantes del Centro Universitario de la Costa Sur de la Universidad de Guadalajara. Julio

y Clara, gracias por su amistad y por ese recibimientos que nos dieron cuando llegamos a Coatepec.

A aquellos que ya partieron; Araceli, Foncho, Pablo, Pepe, Olguín, Pedro, Lorenzo, Eva, Esperanza y Estela, algún día nos reuniremos nuevamente.

## AGRADECIEMIENTOS

De una manera especial, agradezco a mi tutor académico, Dr. Exequiel Ezcurra por su confianza que depositó en mi para la realización de esta tesis. Sus consejos, enseñanzas, paciencia, y amistad, fueron siempre fuente de motivación que hizo posible la culminación de este trabajo, sin su apoyo no hubiera sacado adelante este trabajo. De igual manera, agradezco a mis asesores, al Dr. Miguel Martínez Ramos y a la Dra. Elena Alvarez Buylla por todo el apoyo que me brindaron, sus comentarios y consejos fueron siempre acertados y muy estimulantes, por su confianza y su amistad, muchas gracias.

Agradezco también como sinodales a los doctores, Ezequiel Ezcurra, Miguel Martínez Ramos, Elena Álvarez-Buylla, Edmundo García Moya, Mauricio Quesada, Santiago Arizaga Pérez y a Bruce F. Benz, por sus comentarios y sugerencias que hicieron a esta tesis. Su buena disposición de llevar a cabo la revisión de la tesis de una manera rápida, fue para mi estimulante para concluir esta tesis.

Debido a que siempre radique fuera del D.F. numerosas fueron las veces en las que tuve que viajar a la UNAM-D.F. para hacer trámites y cortas estancias, agradezco sinceramente a  Ángela Saldaña, Ángela Acosta y a Juan Sarquís por brindarme su hospitalaria amistad. No puedo dejar de agradecer al maestro Paquín por las vueltas que se dio a la UNAM para hacer algunos trámites.

Quiero agradecer a mis viejos amigos, a mis "paisanos" por su amistad y por haberme apoyado desinteresadamente en aquellos difíciles días de estudiante en el trópico húmedo, tengo una deuda con ustedes.

## Reflexión y despedida

La honestidad, los principios y los valores
son elementos que tienen de pie a los grandes hombres.
Puedes tener logros, premios y mas reconocimientos,
pero si lo tienes por el sudor de los demás
o de una manera fraudulenta,
el polvo del olvido los borrará.
No compres ni vendas a tus amigos como viejos cachivaches,
Pues a los comprados, otros los comprarán
y los que vendiste jamás regresarán.
No cambies la amistad sincera con espejos y piedras,
es mas valioso el diamante de la amistad sincera.
No prostituyas tu ideales para lograr con rapidez tus metas,
porque jamás volverás a ser tu propia esencia.
La lucha por los cambios se da en la trinchera que te corresponde,
construye y lucha en la tuya sin abatirla antes de la gran lucha.
No hay cosa mas bella que el amor y una compañía sincera.

Lázaro R. Sánchez Velásquez

Verano del 2000

# CAPÍTULO I

## RESUMEN

Los estudios ecológicos y demográficos son una herramienta útil para la conservación de especies raras, amenazadas o de importancia económica. Uno de los principales objetivos de la Reserva de la Biosfera Sierra de Manantlán es la conservación *in situ* de las poblaciones del teocintle *Zea diploperennis*. En este estudio se presentan los resultados sobre aspectos ecológicos y demográficos del pariente silvestre del maíz, *Zea diploperennis* y fue dividido en tres fases. La primera fase consistió en contestar las siguientes preguntas:¿El principal banco de frutos del cuál depende la incorporación, se encuentra en la parte aérea de la planta o en el suelo?. ¿Existe una relación entre el estado sucesional y el banco de frutos de *Zea diploperennis*?. La segunda fase describe la estructura, el flujo de individuos genéticos ("genets") y tallos (en este caso es una unidad clonal llamada también "ramet") de siete poblaciones de *Zea diploperennis* durante dos estaciones de crecimiento. Se evalúa la relación entre varios factores del medio (altitud, exposición, pendiente y tipo de suelo) y el estadio sucesional, y atributos demográficos (tasa de incremento de individuos genéticos y tallos, y número de individuos incorporados). También se explora la relación entre la edad y la tasa de mortalidad de individuos. La tercera fase tuvo como objetivos la descripción y análisis del efecto de dos perturbaciones antropógenas (roza-tumba y quema *vs.* roza tumba sin quema) sobre algunas características demográficas básicas de *Zea diploperennis*. En particular el esfuerzo se concentró en: a) describir cambios de la población durante cinco años en cuadrantes bajo diferentes regímenes de perturbación, b) Estimar la contribución relativa de diferentes estados de vida al crecimiento de la población bajo diferentes secuencias de perturbación, y (c) identificar

regímenes de perturbación que puedan permitir la persistencia de poblaciones de *Zea diploperennis* en el tiempo.

Los resultados señalaron que: (1) Las poblaciones de *Zea diploperennis* presentan tanto un banco de frutos en la parte aérea como en el suelo, siendo la primera cuatro veces mayor que la segunda ($\chi^2 = 4.2$, p=0.04). Los estadios sucesionales más avanzados fueron los que presentaron una mayor cantidad de frutos en el suelo (Duncan p=0.05). (2) La población de tallos fluctuó mas a través del tiempo, mientras que los individuos coetáneos (cohortes de genets) disminuyeron. La dinámica de las poblaciones de individuos genéticos siguió un ritmo estacional con un tamaño máximo de la población al inicio de la temporada de las lluvias. Se encontró una relación lineal significativa entre la mortalidad de la cohorte y su edad, las mas jóvenes presentaron una mayor proporción de mortalidad que las mas viejas. La tasa de mortalidad fue mayor durante la temporada de lluvias. (3) Las curvas de sobrevivencia de las cohortes que se registraron desde fruto fue de tipo III, mientras que las cohorte de tallos fue de tipo I. (4) Los efectos del perturbación exhiben diferencias significativas en el número de tallos, mazorcas y producción de frutos por mazorca., siendo mas alto cuando la roza-tumba y quema fue aplicada. (5) Las perturbaciones aplicadas causaron un aumento de casi el 100% del valor de $\lambda$, elevándola a valores cerca o mayores a 1, siendo la permanencia el estado mas importante en contribución a los valores de $\lambda$. Lo anterior sugiere que la competencia asimétrica intraespecífica podría ocurrir, *i. e.*, los individuos establecidos al inicio son los responsables de la supresión e incorporación cuando la población no es perturbada. (6) Si las poblaciones no son perturbadas, entonces la especie será localmente extinta. Para asegurar la permanencia de una población de *Z*.

*diploperennis* a largo plazo, este deberá manejarse con perturbaciones de al menos uno
cada cinco años.

## SUMMARY

Ecological and demographic studies are a useful tool for conservation of species
that are rare, threatened or economically important. One of the principle objectives of the
Sierra de Manantlán Biosphere Reserve is the *in situ* conservation of the populations of the
*teosinte Zea diploperennis*. In this study are show the results of ecologic and demographic
aspects of the wild relative of corn, *Zea diploperennis*, and were divided into three phases.
The first phase consisted of answering the following questions: of the principle fruits pool,
which does the recruitment depend on, is it found in the part of the plant above ground or
underground? Does a relationship between the successional stage and the fruits pool of *Zea
diploperennis*? The second phase describes the structure, the flow of genets and ramets of
seven populations of *Zea diploperennis* during two season of growth. The relationship
between some environmental factors (altitude, exposure, slope and type of soil) and the
successional stage and demographic attributes (growth of genets and ramets, and
recruitment) is evaluated. Also, the relationship is explored between the age and the
mortality rate of genets. The third phase had the objectives of description and analysis of
the effect of two anthropogenic perturbation (slash and burn vs. slash without burn) on
some basic demographic characteristics of *Zea diploperennis*. In particular the effort
concentrated in: a) describing the changes in population during five years in plots under
different perturbation regimens, b) Estimate the relative contribution of different life stage
on the population growth under different sequences of perturbation and c) identify the

regimens of perturbation that would permit the persistence of populations of *Zea diploperennis* in time.

The results showed that: (1) the populations of *Zea diploperennis* present as much a fruits pool in the part above ground as the part underground, being the first four times more than the second ($\chi^2 = 4.2$, p=0.04). The oldest successional stages were who that presented a major quantity of fruits underground (Duncan p=0.05). (2) The population of ramets fluctuated more over time while the genets cohorts diminished. The dynamic of the populations of genets followed a seasonal rhythm with a maximum size of the population at the begin of the rainy season. A linearly significant relationship was found between the mortality of the cohort and their age, the youngest presenting a larger proportion of mortality than the older. The mortality rate was highest during the rainy season. (3) The survival curves of the cohorts that were registered from fruit was type III, while the cohort of ramets were type I. (4) The effects of perturbation showed significant differences in the number or stems, ears and production of fruits per ear, being higher when the slash-burn was applied. (5) The perturbation applied caused an increase of almost 100% of the value of $\lambda$, increasing it to values close to or higher than 1, being the permanence the stage most important in the contribution of the values of $\lambda$. The previous suggests that the asymmetric competence intraspecific could occur, *i.e.*, the genets established at the begin are those responsible for the suppression and recruitment when the population is not perturbated. (6) If the populations are not perturbated, then the species would be extinct locally. To assure in the long term the permanence of *Z. diploperennis* populations, this should be managed with perturbations of at least one every five years.

# CAPÍTULO II

## INTRODUCCIÓN

Los estudios ecológicos básicos y demográficos pueden aportar elementos importantes para la conservación *in situ* de especies amenazadas, raras, en peligro de extinción y plantas de importancia económica (Harvey 1985; Brussard 1991; Owen y Rosentreter 1992; Olmsted y Álvarez-Buylla 1995). *Zea diploperennis* es un pariente silvestre del maíz y fue "la punta de lanza" para la creación de la Reserva de la Biosfera Sierra de Manantlán en Jalisco, México, lugar endémico de este teocintle. Esta especie tiene potencial para el mejoramiento genético del maíz y su conservación es uno de los objetivos de la reserva. Esta especie esta asociada a estadios iniciales de la sucesión y se requieren conocimientos para ejecutar un programa efectivo que asegure su conservación *in situ*.

*Zea diploperennis* es una especie perenne, rizomatosa, heliófila, sus tallos pueden medir hasta tres metros de altura y es parecido al del maíz. Su crecimiento clonal es de tipo falange, donde los tallos, en la mayoría de los casos, no se separan del tallo madre y los individuos genéticos son policárpicos con tallos monocárpicos.

Incendios localizados ocurren cada año en la Sierra de Manantlán, como resultado del escape del fuego del sistema tradicional agrícola de maíz, llamado coamil (roza-tumba-quema). Las perturbaciones inducidas por el humano son también creados por la ganadería extensiva en la vegetación natural. El sistema de coamil mezclado con *Zea diploperennis* ha exhibido, bajo condiciones experimentales, que los individuos de este último se ven favorecidos por estas perturbaciones. Sin embargo, el efecto global de la perturbación a nivel de población y bajo condiciones naturales no ha sido evaluado. Adicionalmente, especies de árboles como *Magnolia iltisiana* y la comunidad entera de bosque mesófilo de montaña parecen ser sensibles a incendios y/o aprovechamiento pecuario.

5

La Estación Científica Las Joyas, localizada dentro de la zona núcleo de la Reserva de la Biosfera Sierra de Manantlán tiene las segundas poblaciones mas grandes de *Zea diploperennis*. Estas poblaciones han sido excluidas del ganado y protegidas contra incendios forestales desde 1988, como parte de las principales políticas de protección del área núcleo Manantlán-Las Joyas, y en la conservación de la poblaciones existentes de *Zea diploperennis*. Basado en la evidencia de que el fuego y la ganadería extensiva favorecen el desarrollo de *Zea diploperennis*, mientras que al mismo tiempo estas perturbaciones pueden limitar la preservación de otras especies y comunidades, opciones de manejo son necesarias para armonizar la conservación del teocintle con otros tipos de perturbaciones antropógenas.

Este trabajo consigna tres fases de un estudio ecológico y demográfico de poblaciones naturales de *Zea diploperennis*. La primera fase cosiste en dar respuesta si el principal banco de frutos está en el suelo o en la parte aérea y muerta de la planta y conocer si hay o no relación entre el estadio sucesional y el banco de frutos. La segunda fase describe la estructura y el flujo de siete poblaciones de individuos genéticos y tallos de *Zea diploperennis*. También se evalúa la relación entre varios factores del medio como; altitud, exposición, pendiente y tipo de suelo y estadio de sucesión *versus* los atributos demográficos de individuos genéticos y tallos. La tercera fase tuvo como objetivos la descripción y análisis del efecto de dos perturbaciones antropogenias: roza-tumba y quema *vs.* roza-tumba sin quema, sobre algunas características demográficas de *Zea diploperennis*.

# CAPÍTULO III

# DINÁMICA ESTACIONAL DEL BANCO DE FRUTOS DEL TEOCINTLE Zea diploperennis (GRAMINEAE)

NOTES

# Dinámica Estacional del Banco de Frutos del Teocintle
## *Zea diploperennis* (Gramineae)

*Palabras clave: banco de semillas; conservación; sucesión; teocintle;* Zea diploperennis.

EL BANCO DE SEMILLAS O FRUTOS representa una de las fases más importantes del ciclo de vida de muchas especies de plantas, ya que en esta fase suceden procesos (depredación, germinación y dispersión) que pueden repercutir directamente en el tamaño de las poblaciones futuras (Guevara 1977, Harper 1977). El banco de semillas puede estar en el suelo o raramente en la parte aérea de algunas especies de plantas (Baker 1989), sin embargo existe aún información poco precisa sobre el papel que juega el banco de semillas de la parte aérea de las plantas progenitoras (Grime 1989). Los estudios de los bancos de semillas en condiciones naturales pueden ser útiles para la conservación de especies de plantas raras o en peligro de extinción, principalmente para aquellas que dependen de la propagación por semillas para invadir nuevos lugares o para mantenerse en un lugar determinado. La cantidad y calidad del banco de semillas varía a través de las estaciones del año (Grime 1982, Ortiz-Arrona 1992). Este trabajo describe la dinámica estacional de los bancos de frutos de *Zea diploperennis* Iltis, Doebley, Guzman & Pazy pertenecientes a tres áreas de diferente estado sucesional. Con el objeto de fortalecer las recomendaciones de manejo para su conservación *in situ* contestamos las siguientes preguntas: ¿El principal banco de semillas o frutos del cuál depende el reclutamiento, se encuentra en la parte aérea de la planta o en el suelo? ¿Existe una relación entre el estado sucesional y el banco de frutos de *Zea diploperennis*?.

*Zea diploperennis* (Gramineae) es una planta rizomatosa iterópara con tallos semelparos. Su crecimiento clonal es de tipo falange (Hutchings & Bradbury, 1986) y los individuos pueden vivir más de 8 años (Sanchez-Velásquez 1992, ver Iltis *et al*. 1979 para su descripción taxonómica). Las mazorcas tienen de 6 a 11 frutos (cada fruto contiene una semilla), éstos son dispersados principalmente por barocoria y en su mayoría ocurre de diciembre a enero, con la excepción de los dos frutos más cercanos al pedúnculo que permanecen durante la temporada de sequía (aprox. enero–junio); al inicio de las lluvias éstas semillas son dispersadas a través de la muerte y caida del tallo, la germinación también ocurre al inicio de las lluvias (obs. pers.). Esta especie es endémica de la Reserva de la Biósfera Sierra de Manantlán (RBSM) y está asociada al cultivo del maíz, cuyas prácticas favorecen su crecimiento y desarrollo de los individuos (Sánchez-Velásquez *et al*. 1992). Mantiene su presencia en áreas de cultivo abandonados (aprox. 360 ha en toda la RBSM), dominando las primeras etapas de la sucesión pero permitiendo la existencia de especies asociadas en etapas posteriores (Benz *et al*. 1990). Las estructuras de las poblaciones están dominadas por los primeros individuos que invadieron las áreas (L. Sánchez-Velásquez, com. pers.). Esta especie es resistente a las siete principales enfermedades que atacan al maíz (Nault & Findley 1982a, 1982b) y al cruzarse con éste, bajo condiciones naturales, producen híbridos fértiles (Iltis *et al*. 1979, Benz *et al*. 1990, obs. pers.). La importancia de la conservación de *Z. diploperennis* radica en que ésta especie tiene un potencial para el mejoramiento genético del maíz y se pueden obtener ahorros de hasta 6.82 billones de dolares anuales (Fisher & Hanemann 1985).

Este trabajo se realizó en siete áreas de cultivo de maíz abandonadas desde hace 7 (3 áreas), 12 (2 áreas) y 17 (2 áreas) años, éstas las agrupamos y denominamos como estados sucesionales 7 (con 4 ha), 12 (con 22.27 ha) y 17 (con 3.54 ha), respectivamente. En cada área había una poblacion de *Z. diploperennis* y se localizan en la Estación Científica Las Joyas (ECLJ) de la RBSM (Pérez 1991), Jalisco, México (19°35'42"–19°37'40"N y −103°15'02"–104°37'40"O). Las superficies presentan una topografía muy irregular; el estado 7 presenta pendientes de 0 a 20(%) y los estados 12 y 17 entre 10 y 20(%), y las altitudes son de 1960 a 2000 m, de 2000 a 2030 m y de 1960 a 2020 m, respectivamente (L. Sánchez-Velásquez, com. pers.). Todas las poblaciones estan rodeadas de bosque de *Pinus* y bosque mesófilo de montaña (Rzedowski 1977), la distancia entre ellos varía de 800 m a 1000 m. La temperatura media anual es de 18° C con una precipitación pluvial anual de 1500 a 1800 mm, con régimen de lluvias de junio a octubre y lluvias estacionales en invierno; neblinas son frecuentes excepto en la temporada más seca que corresponde a marzo y mayo (Saldaña & Jardel 1992).

De abril de 1990 a abril de 1991 se tomaron aleatoriamente, cada cuatro meses, 21 muestras de

suelo (tres en cada uno de los estados sucesionales), 9, 6 y 6 en los estados sucesionales 7, 12 y 17, respectivamente; la unidad de muestreo fue de 30 cm (largo y ancho) × 5 cm de profundidad. El uso de ésta profundidad está respaldada por el trabajo de Sánchez-Velásquez & Lorente-Adame (1993), quienes demostraron que la máxima profundidad en donde se encuentran frutos de Z. *diploperennis* es a 10 cm, la cual fue raro y la principal cantidad de semillas se encuentra arriba de los 5 cm de profundidad. En cada una de las muestras se removió la hojarasca y el material rocoso; después se guardó en una bolsa plástica negra con los datos del sitio. De uno a dos días después y en el laboratorio se separaron los frutos de Z. *diploperennis* tamizando la muestra con una malla de luz de 4 mm. A los frutos completos y sin daño aparente se pusieron a imbibición durante 24 horas en cajas de Petri con algodón y papel filtro humedecidos con agua destilada. Después se procedió a bisectarlos longitudinalmente y una mitad de cada fruto se les realizó la prueba de viabilidad con una solución de cloruro de tetrazolium al 0.1(%) en solución buffer (pH 7±0.1, solución de fosfato de sodio y de potasio), colocándolas durante tres horas en una cámara oscura de una incubadora con una temperatura aproximada de 30°C. Los embriones coloreados de rojo cereza en las partes vitales se consideraron viables (Moreno 1984).

Para observar la remoción (proceso que puede implicar tanto dispersión como depredación) y germinación de frutos de Z. *diploperennis*, se tomaron de tallos escogidos aleatoriamente 2800 frutos (89 ± 4 porciento de viabilidad) en la colecta de enero de 1990. Esta muestra se subdividió en 14 grupos de 200 (resultando una densidad de 5000 frutos por m²), cada grupo se colocó sobre cuadros de malla de aluminio de 22 × 22 cm (con 1 mm de diámetro de luz), ésto con el objetivo de no confundirlos con posibles frutos enterrados. Esta muestras se colocaron aleatoriamente (abril de 1990) en pequeñas áreas (en ausencia de tallos aéreos de Z. *diploperennis*) 6, 4 y 4 muestras en los estados 7, 12 y 17, respectivamente. Se aseguraron los cuadros de malla sobre el piso con un clavo en cada uno de los extremos y se cubrieron los frutos parcialmente con una capa de suelo. La revisión de las muestras se hizo en abril, mayo y agosto de 1991. Un individuo puede llegar a producir más de 1400 frutos, esto implica que en el suelo podemos encontrar más de 5000 frutos por m².

Con el objeto de validar la hipótesis de que la principal fuente de frutos de Z. *diploperennis* está en la parte aérea de la planta (o sea, los frutos basales que no caen sino hasta poco después de las primeras lluvias) y no en el suelo, se realizó otro muestreo en mayo de 1992 (antes de inicio de lluvias y poco antes de la época de germinación de los frutos que va de julio a principios de agosto, L. Sánchez-Velásquez, com. pers.). Para ésta parte del experimento se eligieron los estados 7 y 12, y en cada uno de ellos se colectaron aleatoriamente cinco muestras de suelo ($N = 10$) de 30 cm (largo y ancho) × 5 cm de profundidad. La parte aérea se muestreó de la siguiente manera, aleatoriamente se distribuyeron cinco cuadros de 30 × 30 cm en cada uno de los estados sucesionales ($N = 10$) y se colectaron todos los tallos aéreos de Z. *diploperennis* dentro de cada cuadro. Los tallos se guardaron en bolsas de plástico negras y un día después en el laboratorio se procedió a contar los frutos que se encontraron en ellos. Tanto los frutos del suelo como los presentes en los tallos se le aplicó la prueba de viabilidad. Los frutos se clasificaron en viables (frutos con endospermo y embrión vivo), no viables (frutos con endospermo y embrión muertos), depredados (frutos con agujeros y sin endospermo y embrión) y abortados (frutos sin endospermo y embrión).

En el análisis estadístico, el número de frutos de las muestras de suelo fueron comparados entre los diferentes meses de cada estado sucesional a través del proceso GLM de dos factores de SAS ver. 6.03 (1988), y con GLMs de un factor se compararon los frutos entre los diferentes meses y entre los diferentes estados sucesionales; el número de frutos se transformaron a escala $\log_{10}$ (Zar 1984) y después se analizaron con comparaciones múltiples del proceso Duncan (Proc MEANS de SAS). El experimento de remoción y germinación se analizó con el proceso de GLM de dos factores de SAS; los valores porcentuales de la remoción y germinación del mes de agosto (obtenidos a través de $Pr = r/200$, donde Pr es el valor porcentual de remoción y r es el número de frutos removidos, y $Pg = g/200$, donde Pg es el valor porcentual de la germinación y g es el número de frutos germinados) fueron transformados por raíz cuadrada y posteriormente arcoseno (Zar 1984); Proc MEANS Duncan de SAS fue usado las comparaciones multiples. Los datos del banco de frutos del suelo vs. parte aérea (tallos) se compararon a través de la prueba de Mann-Whitney (Zar 1984) con aproximación Chi² (SAS 1988, proc NPAR1WAY).

El número de frutos encontrados en el suelo fluctúa durante el período de un año, y el patrón general es similar en las tres estados secesionales estudiados; disminuyen en agosto y aumentan en diciembre (Fig. 1a, 1b). Los valores promedios y error estandar de la media de las muestras de suelo se muestran en la
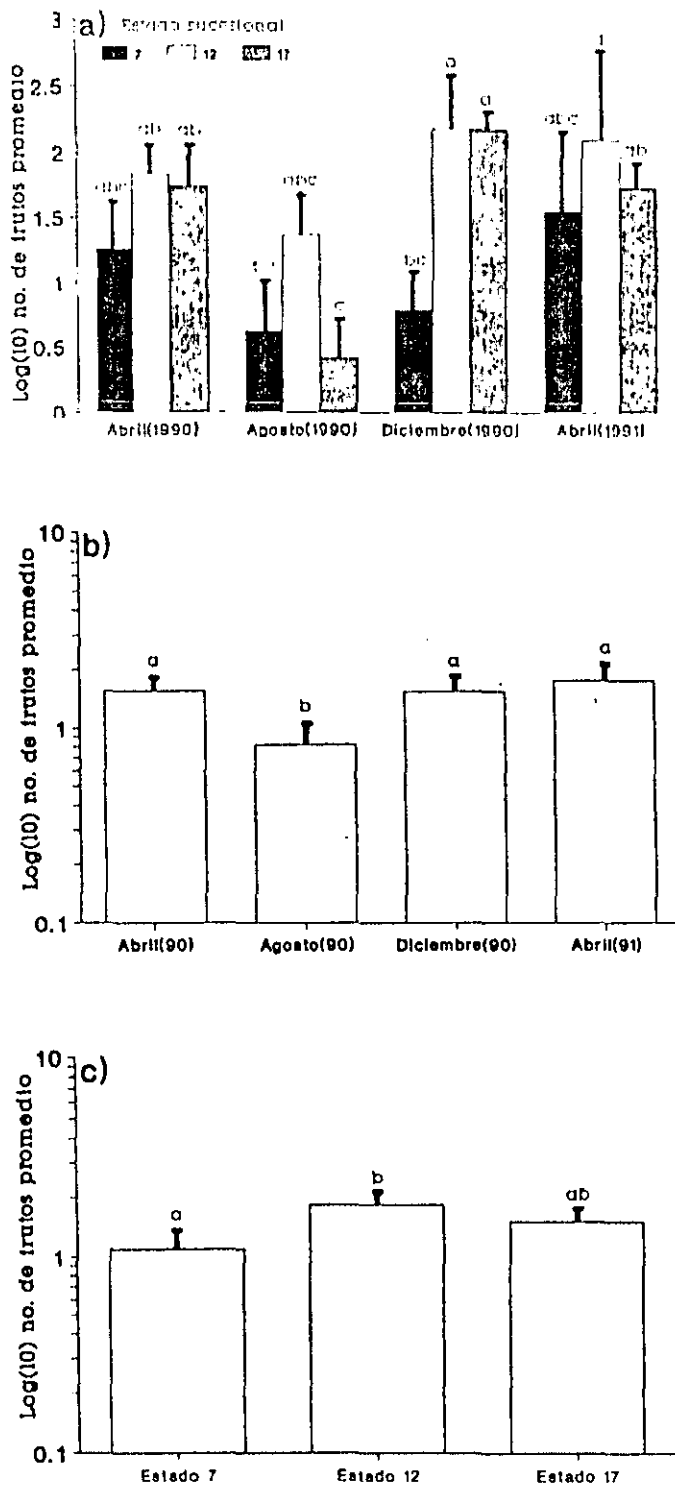
FIGURA 1.    Comparaciones entre el numero de frutos promedio (valores transformados en $\log_{10}$, por; a) estado sucesional-mes, b) por mes y c) por estado sucesional (a: $P < 0.002$; b: $P = 0.009$; c: $P = 0.02$). Letras iguales dentro de cada una de las gráficas señala que no hay diferencias significativas (Duncan, $P = 0.05$).

10

figura 1. Se evidencían diferencias significativas ($F = 4.17$, gl $= 5,69$ $P < 0.002$) entre algunos meses de los estados sucesionales (Duncan $P = 0.05$, Fig. 1a).

Los datos comparados entre meses mostraron ser significativamente diferentes ($F = 4.21$, gl $= 3,69$ $P = 0.009$), agosto de 1990 fué significativamente menor a los otros meses (Duncan $P = 0.05$, Fig. 1b). Los datos también se compararon entre estados sucesionales, y se observaron diferencias significativas ($F = 4.12$, gl $= 2,69$ $P = 0.02$) entre los estados 7 y 12 (Duncan $P = 0.05$, Fig. 1c). Nosotros inferimos que la disminución de frutos en el mes de agosto (Fig. 1b) se debe probablemente a que éste es el mes posterior al inicio del periodo de lluvias así como de la germinación y establecimiento de plántulas de Z. *diploperennis* (Jiménez 1991, Sánchez-Velásquez *et al.* 1992, obs. pers.), por lo tanto se encuentran menor cantidad de frutos en el suelo. Agosto es el mes en que finaliza la germinación de frutos de Z. *diploperennis*. Es evidente de que el banco de frutos de Z. *diploperennis* es de tipo persistente, ésto se demuestra por que aún después de la dispersión y germinación, persisten semillas en el suelo, i. e., en el mes de agosto.

La remoción de frutos fue alta. Después de tres meses ésta fué del 97.8(%) en las tres áreas, la germinación fue menos del 2.2(%). En agosto (1990) observamos que los frutos no germinados fueron removidos en su totalidad. Se encontraron diferencias significativas entre el estado sucesional *vs.* la remoción ($F = 111.2$, gl $= 6,7$ $P = 0.0001$) y *vs.* germinación ($F = 6.5$, gl $= 6,7$ $P = 0.0133$). La remoción fué significativamente mayor en el estado más joven (estado 7 $= 183.2 \pm 10.7$, estado 12 $= 178.3 \pm 13.03$ y estado 17 $= 176.3 \pm 14.14$), mientras que para la germinación lo fue el estado 12 ($4.3 \pm 2.5$), los estados 7 ($0.5 \pm 0.3$) y 17 ($2.25 \pm 1.4$) no fueron significativamente diferentes en la germinación (Duncan $P = 0.05$). Las diferencias significativas entre el número de frutos encontrados en el suelo y porcentage de frutos germinados no nos presenta un patrón claro entre ellos y el estado sucesional. Solamente el porcentage de remoción nos señala que el estado más joven presenta el mayor porcentage de remoción.

La alta remoción observada de frutos, y quizá la depredación en las áreas estudiadas se debe probablemente a la presencia de *Reithrodonthomys fulvescens*, al revisar los nidos de éste roedor, los cuales estan hechos con tallos de Z. *diploperennis* y otras ramas de plantas asociadas, se encontraron tanto frutos completos como abiertos, éstos últimos estaban agujerados de igual forma que los encontrados en los cuadros de malla y en el banco de frutos del suelo.

Las poblaciones de Z. *diploperennis* presentan un banco de semillas que se distribuye tanto en la parte aérea de la planta como en el suelo. La mayor parte del banco de frutos está en la parte aérea de la planta ($35.3 \pm 14.8$ proyectada en $0.09$ m$^2$), es cuatro veces más que el banco de frutos en el suelo ($5.2 \pm 1.4$ proyectada en $0.09$ m$^2$) y son significativamente diferentes (Kruskal-Wallis aproximación Chi$^2$ = $4.2$, gl $= 1$, $P = 0.04$). No hubo diferencia significativa en número de frutos no viables entre las muestras del suelo y la muestra de los tallos, $5.2 \pm 0.95$ y $4.8 \pm 1.7$, respectivamente (Kruskal-Wallis Chi$^2$ = $0.83$, gl $= 1$, $P = 0.36$). Encontramos diferencias significativas entre el número de frutos abortados de las muestras de suelo ($0.0$) y las muestras de los tallos ($25.7 \pm 8.5$). Los frutos abortados que sólo se observaron en la parte aérea (estos generalmente son pequeños con un pericarpio delgado y frágil), quizá no se observaron en las muestras de suelo por tener mayor probabilidad de biodegradación y fragmentación. Este tipo de frutos en la parte aérea estan protegidos de la intemperie por las brácteas de las mazorcas.

Los frutos que permanecen durante la época de sequía en la parte aérea de la planta, forman la principal fuente potencial de reclutamiento de las poblaciones de Z. *diploperennis*. Una vez que inician las lluvias (junio) los tallos muertos (tallos semelparos) caen y liberan los frutos para fórmar parte del banco de frutos del suelo e inmediatamente germinar. Es posible que este proceso adaptativo favorezca a la planta para escapar a los roedores que ya han sido reportados en éstas áreas, estos son; *Reithrodontomys fulvescens*, *R. sumichrasti*, *Peromyscus boylli*, *P. spicilegus*, *P. hyloceles*, *Oryzomys couesi*, *O. melanotis*, *Sigmodon alleni* y *Neofoma alleni* (Galván 1992).

Otros trabajos han señalado la importancia del banco de semillas en la parte aérea de las planta progenitoras en la dinámica poblacional (Simpson *et al.* 1989) como en algunos árboles del género *Pinus* y árboles australianos de los géneros *Callistemon* y *Melaleuca* (Myrtaceae) (ver Grime 1989 y Baker 1989). Con fundamento al patrón discontínuo de dispersión de semillas, en el que la parte aérea de la planta juega un papel importante en el banco de semillas o frutos (Baker 1989), postulamos que algunas gramíneas, principalmente el gremio de los teocintles, presentan esta estratégia adaptativa que les permite escapar a los depredadores en el suelo.

Recomendaciones de manejo. Los resultados de este estudio sugieren que el teocintle *Zea diploperennis*

11

presenta un banco de frutos persistente. Sin embargo, la mayoría de los frutos caen de los tallos y son removidos inmediatamente o germinan. Los que se mantienen adheridos a los tallos semelparos soportan la remoción y la época de sequía, formando así la principal fuente de frutos, por lo que el banco de frutos está principalmente en la parte aérea y muerta de la planta.

Los resultados nos permiten inferir que entre más corto sea el período de sequía mayor será la probabilidad de sobrevivencia de los frutos, ya que así germinarán y escaparán a la depredación por roedores. Es evidente que un número pequeño de frutos escapan a la depredación y éstos tengan el potencial para formar un banco de frutos en el suelo. Sánchez-Velásquez y Lorente-Adame (1993) demostraron éste potencial en diferentes hábitats y profundidades del suelo, *i.e.*, entre más enterrada esté el fruto (hasta 10 cm) mayor probabilidades de sobrevivencia tendrá y a menor dosel vegetal menor será la sobrevivencia. Para repoblar áreas con *Zea diploperennis* o crear nuevas áreas, recomendamos que las nuevas áreas o aquellas en las que comienza la extinción local (L. Sánchez-Velásquez, com. pers.), se aplique la roza-tumba-quema ("slash-and-burn") o roza-tumba sin quema (Sánchez-Velásquez *et al.* 1992) y que los frutos, previamente colectados de diferentes poblaciones (para asegurar una amplia diversidad genética) se dispersen al "voleo" poco antes o inmediatamente después de las primeras lluvias, con el objeto de que escapen a los depredadores y asegurar así la emergencia de nuevas plántulas. Esta recomendación se hace para la segunda localidad más grande con poblaciones de *Z. diploperennis,* la Estación Científica Las Joyas. En este lugar ha sido excluido el ganado bovino (principal dispersor) desde 1988 y se ha eliminado el uso de la práctica tradicional del cultivo del maíz llamada roza-tumba-quema; actividades asociadas al desarrollo y mantenimiento de las poblaciones de *Z. diploperennis* (Iltis *et al* 1979, Benz *et al.* 1990, Sánchez-Velásquez *et al.* 1992).

BAKER, G. H. 1989. Some aspects of the natural history of seed bank. *In* L. M. A. Leck, T. V. Parker, and R. L. Simpson (Eds.). Ecology of soil seed banks, pp. 9–21. Academic Press, San Diego, California.

BENZ, B. F., L. R. SÁNCHEZ-VELÁSQUEZ, AND F. J. SANTANA-MICHEL. 1990. Ecology and ethnobotany of *Zea diploperennis*: preliminary investigations. Maydica 35: 85–98.

FISHER, A. C., AND W. H. HANEMANN. 1985. Option value and the extinction on species. Calif. Agric. Exp. Stn. Bull.

GALVÁN, C. A. L. 1992. Patrones ecológicos de las comunidades de pequeños roedores en tres tipos de hábitats en la Estación Científica Las Joyas. Tesis de licenciatura. Facultad de Ciencias Biológicas, Universidad de Guadalajara, Jalisco, México.

GRIME, J. P. 1982. Estrategia de adaptación de las plantas y procesos que controlan la vegetación. LIMUSA, México.
————. 1989. Seed banks in ecological perspectives. *In* L. M. A. Leck, T. V. Parker, and R. L. Simpson (Eds.) Ecology of soil seed banks, p.p. xv–xiii. Academic Press, San Diego, California.

GUEVARA, F. E. 1977. Dinámica de poblaciones de semillas de *Cordia elaegnoides* (DC), en una selva baja caducifolia. Tesis de licenciatura. Facultad de Ciencias, Universidad Nacional Autónoma de México. México, D. F., México.

HARPER, J. L. 1977. Population biology of plants. Academic Press, London, England.

HUTCHING, M., AND I. K. BRADBURY. 1986. Ecological perspectives on clonal perennial herbs. Bioscience 36: 178–182.

ILTIS, H. H., J. L. DOEBLEY, R. GUZMÁN, AND B. PAZY. 1979. *Zea diploperennis* (Gramineae): A new teosinte from México. Science 203: 186–188.

JIMÉNEZ, G. G. R. 1991. Crecimiento y desarrollo de *Zea diploperennis* en base a rizomas trasplantados en la Estación Científica Las Joyas. Tesis de Licenciatura. Facultad de Ciencias Biológicas, Universidad de Guadalajara, Jalisco, México.

MORENO, E. M. 1984. Análisis físicos y biológicos de semillas agrícolas. Instituto de Biología, Universidad Nacional Autónoma de México. México, D. F., México.

NAULT, L. R., AND W. R. FINDLEY. 1982a. *Zea diploperennis*: a primitive offers new traits to improve corn. Desert Plants 2: 203–205.

12

————, AND ————. 1982b. Update on perennial corn discovery: rare find has interesting potential. Crops Soils Mag., March: 10–13.

ORTÍZ-ARRONA, C. I. 1992. Banco de semillas del suelo en el bosque mesófilo de montaña de Las Joyas, Sierra de Manantlán, Estado de Jalisco. Tesis de licenciatura. Facultad de Ciencias Biológicas, Universidad de Guadalajara, Jalisco, México.

PÉREZ, S. B. 1991. Estudio fitosociológico de *Zea diploperennis* en la Estación Científica Las Joyas, Sierra de Manantlán, Jalisco, México. Tesis de licenciatura. Facultad de Ciencias Biológicas. Universidad de Guadalajara, Jalisco, México.

SALDAÑA, A. A., AND E. J. JARDEL P. 1992. Regeneración natural del estrato arbóreo en bosques subtropicales de montaña en la Sierra de Manantlán, México: Estudios preliminares. Biotam 4: 36–50.

SÁNCHEZ-VELÁSQUEZ, L. R. 1992. *Zea diploperennis*: mejoramiento genético del maíz, ecología y la conservación de recursos naturales. Tiempos de Ciencia 24: 1–8.

————, AND R. G. LORENTE-ADAME. 1993. Sobrevivencia de frutos de *Zea diploperennis* en diferentes hábitats. Biotam 5: 29–34.

————, A. SOLÍS M., E. CORTEZ, R. G. JIMÉNEZ G., A. CÁRDENAS, Y M. P. ROSALES A. 1992. Efecto del cultivo tradicional del maíz sobre el crecimiento y desarrollo de *Zea diploperennis*. Biotam 3(3): 51–58.

SAS. 1988. SAS/Stat User's guide: ver 6.03. SAS Institute, Cary, North Carolina.

SIMPSON, R. L., L. M. A. LECK, AND T. V. PARKER. 1989. Seed banks: general concepts and methodological issues. *In* L. M. A. Leck, T. V. Parker, and R. L. Simpson (Eds.). Ecology of soil seed banks, pp. 9–21. Academic Press, San Diego, California.

**Rogelia G. Lorente-Adame y Lázaro R. Sánchez-Velásquez**

Instituto Manantlán de Ecología y Conservación de la
Biodiversidad, Centro Universitario Costa Sur,
Universidad de Guadalajara. Independencia Nacional No. 151, Ap. Postal No. 64,
Autlán, Jal., 48900, México.

13

# CAPÍTULO IV

# POPULATION STRUCTURE AND ECOLOGY OF A RARE RHIZOMATOUS

# SPECIES OF TEOSINTE Zea diploperennis (GRAMINEAE)

# REVISTA DE BIOLOGIA TROPICAL
## International Journal of Tropical Biology and Conservation

www.ucr.ac.cr                www.ots.ac.cr                www.ots.duke.edu

31 de julio del 2000
RBT- 295-00

## A QUIEN INTERESE

El manuscrito "Population structure and ecology of a tropical rare rhizomatous species of teosinte *Zea diploperennis* (Gramineae)", por Lázaro R. Sánchez-Velásquez, R. Genoveva Jiménez G. And Bruce F. Benz, ha sido aceptado para publicación en la *Revista de Biología Tropical / International Journal of Tropical Biology and Conservation*. Se incluirá en el volumen 48-4, diciembre del 2000. Si quedan detalles pendientes antes de enviarlo a imprenta, se le informará pronto al autor principal. De otra manera, nuestra próxima comunicación corresponderá a las pruebas de imprenta, junto con las cuales se enviará un formulario por si son necesarias separatas adicionales. Las separatas se envían por correo aéreo normal en los días siguientes a la impresión de la revista. Los autores que desean recibirlas por correo certificado, deben enviar *ahora* $2.00 para cubrir los gastos, junto con una nota explicativa.

Atentamente,

Julián Monge-Nájera
Editor

**IMPORTANTE:** Por favor envíenos inmediatamente dos números confiables de fax para recibir allí sus pruebas de imprenta (el segundo es por si falta el primero, lo cual ocurre con frecuencia). Estos números deben ser completos: incluya desde el código de su país hasta cualquier número de extensión. El incumplimiento de esta instrucción causaría que Ud. no pueda corregir la prueba.

01/08/00

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

Lázaro R. Sánchez-Velásquez [1, 2], R. Genoveva Jiménez G.[2] and Bruce F. Benz [2, 3]

[1] Facultad de Ciencias, Universidad Nacional Autónoma

de México, 04510, México D.F. México.

[2] Instituto Manantlán de Ecología y Conservación de la

Biodiversidad, Centro Universitario de la Costa Sur,

Universidad de Guadalajara, Independencia Nacional No. 151.

Ap. Postal No. 64, Autlán, Jal., 48900, México;

Fax + 338 11425

e-mail lsanchez@cucsur.udg.mx

[3] Biology Department, Texas Wesleyan University, Fort Worth,

TX 76105; e-mail benzb@txwes.edu

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 a perennial, shade intolerant and their shoots are architecturally similar to maize. Clonal growth is of the phalanx type. Genets are iteroparous whit shoots semelparous. Study of the demography of seven module and genet populations of *Z. diploperennis* was undertaken in seven sites representing three different stages of old-field succession. Seven permanent one-meter-square plots were randomly established in each site. All genets present initially and those that became established during our study were mapped and labeled according to the 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

16

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 erosion and further degradation.

**Key words**: Initial seedling recruitment, Manantlán, México, population structure, rehabilitation, teosinte, *Zea diploperennis*.

Study of an organism's basic ecology is the first step in conservation planning and decision-making. Such research provides a basis for understanding and documenting critical stages of a species life history. Protecting and maintaining rare and threatened species in their natural habitats is one of the goals of conservation biology (Lesica 1992) and of the Biosphere Reserves in the Man and the Biosphere – United Nations Educational, Scientific and Cultural Organization program (MAB-UNESCO) (Halffter 1988). Species rarity may be caused by evolutionary and historical events that resulted in the present-day distributions, or by existing ecological and genetic factors (Watson *et al.* 1994). Investigating the 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, Brussard 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,

17

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 to three meter shoots are architecturally similar to maize. Clonal growth is of the phalanx type (Hutchings & Bradbury 1986) where modules (epigeal shoots arising from underground hypogeal rhizome) do not separate themselves from the parent shoot. Genets are iteroparous (but their modules are semelparous), reach sexual maturity and are capable of developing more than one module in the first two years (Sánchez-Velásquez & Lorente-Adame 1993, Lorente-Adame & Sánchez-Velásquez 1996).

This paper reports the descriptive phase of a long-term study whose ultimate goal is to 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), Zarzamoro (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 & Harper 1973). The number of modules per genet was recorded monthly from May to December during year one and year two (except for June and September). In May-year one we could differentiate the genets which were born in one past year because they had one, or rarely two, small modules and one or no inflorescence. Cohorts born during our study were could identified easily: in the first-year, the first leaves to emerge have emarginate apices and in following years have an acuminate apex. Births and deaths were recorded according to age and comparisons of the 1, 2, 3 and $\geq$ 4 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

19

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.

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 ($F = 0.31$, $p > 0.05$), 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 (successional stages) 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 ($F = 0.01$, $p >> 0.05$; Table 3a) nor in December year two ($F = 0.04$, $p >> 0.05$; Table 3b). The annual rate of increase of modules was not significantly different ($F = 0.07$, $p >> 0.05$)(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 examples). These were relatively constant from December year one to July year two. Births occurred during May and July in both years but in year one was greater than in year two. Death of genets was most notable in year one during the period from August to October (Fig. 1).

Genets born in different years (before two or more years from initial study, one year before of initial study, and at first and second year from our study) and were distinguishable throughout the duration of the field work (*i.e.*, we had 1, 2, 3, and $\geq 4$ year-old cohorts in year 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.

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, $2.31 \pm 0.4$ and $1.2 \pm 0.1$; genets in December year two/genets in May year one respectively; $F = 8.64$, $p < 0.01$).

DISCUSSION

Only two partial associations were observed, between rate of population increase of genets *versus* type of soil and stage old field succession (Table 2), the genets increase rate was higher in the oldest stage and Ultisols than in younger stages and Alfisols. Ultisols have low fertility and low base content (Boul *et al.* 1993). Our results suggest that *Z. diploperennis* has greater adaptive success in Ultisols than in Alfisols, hence the higher genets increase rate in Ultisols. However, the plasticity phenotypic experiments in different kind of soil are necessary to test this hypothesis.

In all stages of abandonment genets rate of increase was greater than one. These rates resulted in high recruitment in year one. Nevertheless, when we estimated genets rate of increase from December year one to December year two, the values were lower than one (see Tables two and four). Our results suggest that 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 highest rain season appears to favor the clonal growth in all rhizomatous plants species (Abrahamson 1980).

The general trend of genet survivorship curves among populations was similar. Survivorship across cohorts of the same age appeared to be more synchronized than across cohorts of different age but from the same site (Fig. 2). The mortality in *Z. diploperennis* genets, as in other rhizomatous species (Harper 1977, Lovett Doust 1981), declines with age.

The inverse relation between proportional genets mortality and age is likely to be due to asymmetric intraspecific competition (Crawley 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 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 by Hartnett & Bazzaz (1985), that clonal growth and genet survival of herbaceous clonal species (of the initial seedling recruitment type) are inversely related to time of recruitment. That is, long after initial colonization, populations of herbaceous clonal species will be formed mainly by the genets that became established initially, as hypothesized by Benz *et al.* (1990) (see also Kays & Harper 1974, Maddox *et al.* 1989, Eriksson 1993). This suggest that reproduction from seeds is unimportant at these old stages and might not be a viable alternative for achieving population increase.

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 degradation areas with Ultisol soil could be sowed with *Z. diploperennis*. Such activities would achieve two distinct objectives, promote propagation of this rare endemic and reclaim areas that are susceptible to erosion and further degradation.

## ACKNOWLEDGEMENTS

## RESUMEN

Uno de los objetivos de la Reserva de la Biosfera Sierra de Manantlán (Jalisco, México) es la conservación *in situ* del teosinte *Zea diploperennis*. Esta especie es perenne, intolerante a la sombra y su arquitectura es parecida a la del maíz. El crecimiento clonal es de tipo falange. Los genets son iteróparos con tallos semélparos. Se estudió la demografía de módulos y genets de siete poblaciones de *Z. diploperennis* en siete sitios de cultivo abandonados, estos representan tres diferentes estados de sucesión. Siete sitios permanentes de un metro cuadras fueron aleatoriamente distribuidos en cada uno de los sitios. Todos los genets presentes inicialmente y aquellos que se establecieron durante nuestro estudio fueron mapeados y etiquetados de acuerdo al año de establecimiento. 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. Una relación significativa fue obtenida entre la proporción anual de mortalidad de la cohorte y su edad: 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. Como consecuencia, postulamos que la competencia ocurre principalmente durante la estación de lluvias. Se observaron relaciones lineales entre la tasa de incremento de genets *versus* 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*. Con esta rehabilitación se logran dos objetivos; promover la propagación de esta especie endémica, y recuperar áreas que son susceptibles a la erosión y fuerte degradación.

REFERENCES

Abrahamson, W. G. 1980. Demography and vegetative reproduction, p. 89-106. *In* O. T. Solbrig (ed.). Demography and evolution in plant populations. Blackwell Scientific, Oxford.

Aguilera, M. O. & W. K. Lauenroth. 1993. Seedling establishment in adult neighborhoods-intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. J. Ecol. 81: 253-261.

Benz, B. F., L. R. Sánchez-Velásquez & F. Santana-Michel. 1990. Ecology and ethnobotany of *Zea diploperennis*: Preliminary investigations. Maydica 35: 85-98.

Boul, S. W., F. D. Hole & R. J. McCracken. 1993. Soil Genesis and Classification. Trillas, México, D. F.

Boyce, M. S. 1992. Population viability analysis. Ann. Rev. Ecol. Syst. 23: 481-506.

Brussard, P. F. 1991. The role of ecology in biological conservation. Ecol. Applic. 1: 6-12.

Crawley, M. J. 1990. The population dynamics of plants. Phil. Trans. Roy. Soc. Lond. 330: 125-140.

Eriksson, O. 1993. Dynamics of genets in clonal plants. TREE 8: 313-316.

Gilpin, M. E.& M. E. Soulé. 1986. Minimum viable populations: process of species extinction. p. 19-34. *In* M. E. Soulé (ed.). Conservation Biology. Sinauer, Massachusetts.

Halffter, G. 1988. El Concepto de Reserva de la Biosfera. p. 79-111. *In* P. Reyes-Castillo (ed.). El futuro del hombre en la naturaleza. Instituto de Ecología, Publicación No. 24. México.

Harper, J. L. 1977. Population Biology of Plants. Academic, London.

Hartnett, D. H. & F. A. Bazzaz. 1985. The genet and ramet population dynamics of *Solidago canadensis* in an abandoned field. J. Ecol. 73: 407-413.

Harvey, H. J. 1985. Population biology and the conservation of rare species. p. 111-123. *In* J. White (ed.). Studies on Plant Demography, 111-123. Academic, London.

Hernández, V. G. 1998. Efecto de la ganadería extensiva sobre la regeneración arbórea de los bosques subtropicales de montaña en la Estación Científica Las Joyas, Jalisco. Tesis de Biología, Universidad Veracruzana, Xalapa Veracruz, México.

Hoyt, E. 1988. Conserving the wild relative of crops. International Board of Plant Genetics Resources/World Conservation Union/World Wildlife Fund, Rome.

Huenneke, L. F. 1995. Involving academic scientists in conservation research: perspectives of a plant ecologist. Ecol. Appl. 5: 209-214.

Hutchings, M. & I. K. Bradbury. 1986. Ecological perspectives on clonal perennial herbs. BioScience 36: 178-182.

Iltis, H. H., J. F. Doebley, R. Guzmán & B. Pazy. 1979. *Zea diploperennis* (Gramineae): A new teosinte from México. Science 203: 186-188.

29

Jardel, P. E. J. 1991. Perturbaciones naturales y antrópicas y sus influencia en la dinámica sucesional de los bosques de Las Joyas, Sierra de Manantlán. Tiempos de Ciencia 22: 9-26

Jardel, P. E. J. 1992. Estrategia para la conservación de la Reserva de la Biosfera Sierra de Manantlán. Universidad de Guadalajara, Guadalajara Jalisco, México.

Kays, S. & J. L. Harper. 1974. The relation of plant and tiller density in a grass sward. J. Ecol. 62: 97-105.

Langer, R. H., S. M. Ryle & O. R. Jewis. 1964. The changing plant and tiller populations of timothy and meadow fescue swards. I. Plant survival and the pattern of tillering. J. Ecol. 1: 197-208.

Lesica, P. 1992. Autoecology of the endangered plant *Howellia aquiatilis*; implications for management and reserve design. Ecol. Appl. 2: 411-421.

Lorente-Adame, R. G. & L. R. Sánchez-Velásquez. 1996. Dinámica estacional del banco de frutos del teocintle *Zea diploperennis* (Gramineae). Biotropica 28: 267-272.

Lovett Doust, L. 1981. Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*): I. The dynamics of ramet in contrasting habitats. J. Ecol. 69: 743-755.

Maddox, G. D., R. E. Cook, P. H. Wimberger & S. Gardescu. 1989. Clone structure in four *Solidago altissima* (Asteraceae) populations: rhizome connections within genotypes. Amer. J. Bot. 76: 318-326.

Olmsted, Y. & E. R. Alvarez-Buylla. 1995. Sustainable harvesting of tropical trees:

demography and matrix models of two palm species in Mexico. Ecol. Appl. 5: 484-500.

Owen, W. R. & R. Rosentreter. 1992. Monitoring rare perennial plants: techniques for demographic studies. Nat. Areas. J. 12: 32-38.

Pérez, S. B. 1991. Estudio fitosociológico de *Zea diploperennis* en la Estación Científica Las Joyas, Sierra de Manantlán, Jalisco, México. Tesis de Biología, Universidad de Guadalajara, Guadalajara, Jalisco, México.

Pineda-López, Ma. del R. 1988. Efecto de las perturbaciones sobre la estructura y dinámica de los bosques templados de Las Joyas, Sierra de Manantlán". Tesis de Maestría, Instituto Nacional de Investigaciones sobre Recursos Bióticos, Xalapa, Veracruz, México.

Rabinowitz, D., S. Cairs & T. Dillon. 1986. Seven forms of rarity and their frequency in the flora of the British Island. p. 182-204. *In* M. E. Soulé (ed.). Conservation Biology. Sinauer, Massachusetts.

Sánchez-Velásquez, L. R. 1991. *Zea diploperennis*: mejoramiento genético del maíz, ecología y la conservación de recursos naturales. Tiempos de Ciencia 24: 1-8.

Sánchez-Velásquez, L. R., Solís, M. A., E. Cortéz, R. G. Jiménez-G, A. Cárdenas & M. P. Rosales. 1991. Efecto del cultivo tradicional del maíz sobre el crecimiento y desarrollo de *Zea diploperennis*. Biotam 3: 51-58.

Sánchez-Velásquez, L. R. & García-Moya. 1993. Sucesión en los bosques mesófilo de montaña y de *Pinus* de la Sierra de Manantlán, Jalisco, México. Agrociencia 3: 7-26.

Sánchez-Velásquez, L. R. & R. G. Lorente-Adame. 1993. Sobrevivencia de frutos de *Zea diploperennis* en diferentes hábitats. Biotam 5: 29-34.

Sánchez-Velásquez, L. R., J. J. Rosales-Adame, Ma. del R. Pineda-López & Ma. de los A. Saldaña-Acosta. 1996. Descripción cuantitativa de los bosques en la estación científica Las Joyas de la Reserva de la Biosfera Sierra de Manantlán. Bol. Inst. Bot. U. de G. México 4: 79-155.

Sarukhán, J. & J. L. Harper. 1973. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. I. Population flux and survivorship. J. Ecol. 61: 675-716.

SAS. 1988. SAS Stat user's guide for personal computers, version 6.03. SAS Institute, Cary, N.C.

Seaman, J. W. Jr., S. C. Walls, S. E. Wise & R. G. Jaeger. 1994. Caveat emptor: rank transform methods and Interaction. TREE 9: 261-263.

Tear, T. H., J. M. Scott, P. H. Hayward & B. Griffith. 1995. Recovery plans and the endangered species act: are criticisms supported by data? Cons. Biol. 9: 182-195.

Watson, L. E., G. E. Uno, N. A. McCarty & B. Kornkuen. 1994. Conservation biology of a rare plant species, *Eriocaulon kornickianum* (Eriocaulaceae). Am. J. Bot. 81: 980-986.

Wilkes, H. G. 1994. El teosinte en México como modelo para la conservación in situ: un reto. p. 257-270. *In* B. F. Benz (ed.). Biología, ecología y conservación del género *Zea*, Universidad de Guadalajara, México.

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 |
| Last Crop Cultivated | maize | maize | maize and potato | maize, apple, orchard, pear and pasture | maize, apple, pear and orchard | maize, | maize |
| Site size (ha)[b] | 1.55 | 0.78 | 1.65 | 10.69 | 11.58 | 1.66 | 1.88 |

P = Pine forest, PQ= Pine Oak forest, MMF= Montane mesophytic forest, SV= Secondary vegetation. [a] L. Martínez-Rivera, L. Delgado and E. Flores unpub. data., [b] Pérez (1991).

## TABLE 2
*Flux of* Zea diploperennis *genet populations in three different stages of old field succession (mean number of genets in 1 m² and standard error of the mean, within and without value transformed to rank, respectively). In (d) the values were not transformed to rank.*

| 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] |
| $(X \pm S_x)$ | | | |
| 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 | | | |
| $(X \pm S_x)$ | | | |
| (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] |
| $(X \pm S_x)$ | | | |
| 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 | | | |

34

| | | | |
|---|---|---|---|
| (h) Percent survival of genets (g/total number of genets) X 100 | 63 | 58.1 | 61.7 |
| (i) Expected time for complete turnover (yr) $((1.58/100\text{-}h) \times 100)$ | 4.15 | 4.06 | 4.08 |
| (j) Total genets recorded during study | 1090 | 1035 | 1021 |
| (k) Percent annual mortality of all genets during 20 mo $((f/j) \times 100)$ | 62.4 | 76.9 | 63.3 |

Means with superscripts of the same letter indicate no significant difference at $p=0.05$ (SAS, procedure two factors general linear model, means Tukey test).

## TABLE 3

*Flux of* Zea diploperennis *module populations in three different stages of old field succession (mean number of modules in 1 m² and standard error of the mean, within and without value transformed to rank, respectively). In (d) the value were not transformed to rank*
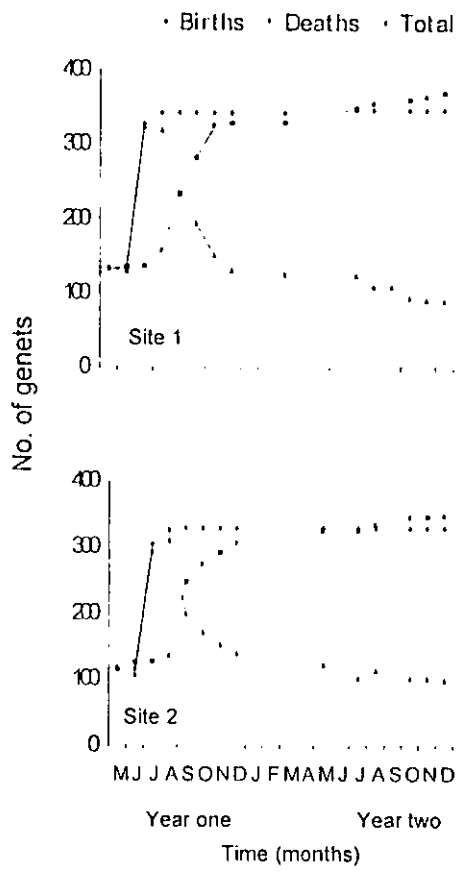
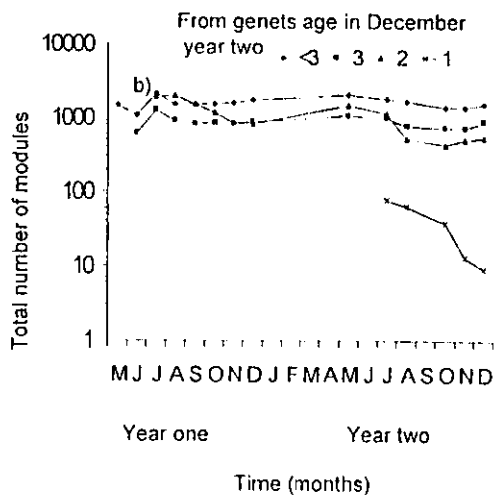| Stage age (yr): | 4 | 14-17 | 17-19 |
|---|---|---|---|
| (a) Mean No. of modules $(X \pm S_x)$ December year one | $72 \pm 9.8$ <br> $25 \pm 2.3^a$ | $70 \pm 13.2$ <br> $25 \pm 4.3^a$ | $64 \pm 8.9$ <br> $25 \pm 3.8^a$ |
| (b) Mean No. of modules $(X \pm S_x)$ December year two | $64 \pm 10.4$ <br> $25 \pm 3.3^a$ | $54 \pm 8.2$ <br> $24 \pm 3.5^a$ | $61 \pm 11$ <br> $25 \pm 4.1^a$ |
| (c) Net change (all plots) | -168 | -224 | -42 |
| (d) Rate of increase (total in year two/ total in year one) | $0.89 \pm 0.1^a$ | $0.94 \pm 0.12^a$ | $0.9 \pm 1^a$ |
| (e) Expected time for complete turnover (yr) $((1.42/100\text{-}h^*) \times 100)$ | 1.42 | 1.42 | 1.42 |
| (f) Maximum no. of modules (all on May of year two) | 1717 | 1273 | 1089 |

Means with superscripts of the same letter indicate no significant difference at p=0.05 (SAS, procedure two factors general linear model, means Tukey test). *Percent survival of modules, all case were zero, because modules are semelparous.

FIGURE LEGENDS

Fig. 1. Total number of genets, cumulative births and cumulative deaths of *Zea diploperennis* in seven 1x1 m quadrates at two sites. The other sites have similar shape.

Fig. 2. a. Survival of genet cohorts of *Zea diploperennis*, total number of genets by age cohorts (1, 2, 3, and $\geq 4$ year-old in December year two) across site. b. Total number of modules as a function of date for *Zea diploperennis* born before two o more year from initial study, genets born in one year before of initial study, and genets born in first and second year from our study, (*i. e.,* in December year two are modules from 1, 2, 3, and $\geq 4$ year-old cohorts) across sites.

· Births   · Deaths   · Total

No. of genets

Site 1

Site 2

M J J A S O N D J F M A M J J A S O N D

Year one          Year two

Time (months)

Age of genets in December
year two ··· ◁ · ·3 · · 2 · · 1

a)

Total number of genets

From genets age in December
year two · ◁ · 3 · 2 · · 1

b)

Total number of modules

M J J A S O N D J F M A M J J A S O N D

Year one                    Year two

Time (months)

39

# CAPÍTULO V

# POPULATION DYNAMICS OF Zea diploperennis, A PERENNIAL HERB: EFFECT OF SLASH AND BURN PRACTICE

# POPULATION DYNAMICS OF *Zea diploperennis*, A PERENNIAL HERB: EFFECT OF SLASH AND BURN PRACTICE

Lázaro R. Sánchez-Velásquez[1,4], Exequiel Ezcurra[3], Miguel Martínez –Ramos[2], Elena Álvarez-Buylla[2] and Rogelia Lorente[1]

[1]Laboratorio de Ecología Aplicada, Instituto Manantlán de Ecología y Conservación de la Biodiversidad, Centro Universitario de la Costa Sur, Universidad de Guadalajara, Apartado Postal 64, 48900 - Autlán, Jalisco, MEXICO

E-mail: lazaro_sanchez@cucsur.udg.mx, lazaro_sanchez@latinmail.com

Present Address: Instituto de Genética Forestal, Universidad Veracruzana, Parque Ecológico El Haya, A.P. 551, Xalapa, Ver., México.

TEL-FAX +28 12 1357

[2]Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, 04510 - México, D. F., MÉXICO

[3]San Diego Natural History Museum, 1788 El Prado, San Diego, California 92101, USA

[4]Author for correspondence

**Summary**

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

2. The patterns of establishment and mortality were qualitatively similar in all populations studied. The cohorts of genets that were followed from germination showed type III survivorship curves, while cohorts of vegetative shoots had type II curves.

3. Numbers of shoots, ears and fruits produced were significantly higher when slash-and-burn disturbance was applied. The massive production of seeds after disturbance support the resource-matching hypothesis. Because permanence is the most important stage in contributing to $\lambda$, 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, $\lambda$ increased to close to 1 or >1. After the first disturbance, $\lambda$ increased by almost 100 %.

5. In almost all situations, with or without disturbance, the persistence loops of *Zea diploperennis* are the most important life history pathways in the relative contribution to fitness. In general, when $\lambda$ increases, sexual growth loops also increase in importance, and persistence loops decrease. Changes in $\lambda$ are not related to changes in vegetative growth loops.

6. If populations of *Z. diploperennis* are not disturbed at lest one every 5 years, the species will go extinct in the wild.

*Keywords*: Disturbances, demography, loop analysis, mast seeding, slash-and-burn.

## Introduction

The study of population regulation and demography in their natural habitats is extremely important for the conservation of rare and endangered species and for the sustainable management of economically important plants (Harvey 1985; Brussard 1991; Owen & Rosentreter 1992; Olmsted & Álvarez-Buylla 1995). Protecting and maintaining rare and threatened species in their natural habitats is one goal of conservation biology (Brussard 1991; Lesica 1992). Although *teosintes* —the wild relatives of maize— have a large economic potential for the improvement of cultivated corn (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 & Ordaz 1987; 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 (see Wellhausen *et al.* 1951; Sánchez & Ordaz 1987; Iltis 1993). *Zea diploperennis* Iltis, Doebley, Guzmán and Pazy, the most recently-described species of 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 geographic range, although it is locally frequent, with crowded populations in discrete patches (see Rabinowitz *et al.* 1986 for a discussion of geographic, ecological, and demographic levels of rarity). Indeed, one of the objectives of the Sierra de Manantlán Biosphere Reserve and the associated Manantlán Institute of Ecology and Conservation of Biodiversity (University of Guadalajara) is the *in situ* conservation of this teosinte (Jardel 1992).

Small-scale fires occur every year in Manantlán, mostly as a result of escaped burning from the *coamil* agricultural system (a slash-and-burn land management technique used by

local peasants or *campesinos*). 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 global effect of disturbances at the population level and under natural conditions has not been evaluated. Additionally, uncontrolled burning and grazing may threaten other rare species in the Manantlán Reserve, such as *Magnolia iltisiana* (Vázquez & Cuevas 1995), as well as whole communities that seem to be sensitive to burning and/or grazing, such as the cloud forests (Pineda-López 1988; Sánchez-Velásquez 1988; Jardel 1991; Saldaña & Jardel 1992; Sánchez-Velásquez & García-Moya 1993).

The Las Joyas Field Station, located within the core area of the Reserve, has the second largest populations of *Zea diploperennis* (the largest populations are in the indigenous community of San Miguel Ayotitlán; see Benz, *et al.* 1990). These populations have been protected from grazing and forest fires since 1988, as part of management policies aimed at the protection of the core area of the reserve and conservation of the existing populations of *Z. diploperennis* (Jardel 1992). Additionally, 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. Studies of populations of a single species under contrasting management conditions (e.g. different successional stages or different intensity of disturbance) can lead to a better understanding of the demographic patterns of successional species than studies made on a single area (Weaver & Cavers 1980; Lovett-Doust 1981; Maddox *et al.* 1989; Watson *et al.* 1994).

Our objective was to analyse and compare the effect of two types of anthropogenic disturbance (slash-and-burn *vs.* slash without burning) on the demography of *Z. diploperennis*. In particular, (a) to describe population changes during five years in plots

under different land disturbance regimes, (b) to assess the relative contribution of different life-history stages to population growth under different disturbance sequences, and (c) to identify disturbance regimes that may enable the persistence of populations of *Zea 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 two meters ($\pm 1$ m) high (Sánchez-Velásquez 1991; Sánchez-Velásquez *et al.* 1992). Clonal growth is "phalanx-type" (*sensu* Clegg 1978; cited in Hutchings & Bradbury 1986), developing radially from the parental shoot with short rhizomes that form a compact circular front. The plants can grow in narrow association with maize fields under traditional *coamil* cultivation (Iltis 1980; 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), Benz *et al.* (1990) and Sánchez-Velásquez *et al.* (1992) 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 recognised (e.g. FAO 1989).

The Sierra de Manantlán Biosphere Reserve is located in the mountains of Southern Jalisco, Mexico. It comprises oak forests in the lower elevations, and pine and montane mixed forests in the higher ranges. Pine stands occupy the drier slopes, while species-rich montane forest communities are found on the wetter areas (Jardel *et al.* unpublished data). The sites where *Zea diploperennis* is found are within montane forest habitats at altitudes ranging from 1900 to 2100 m. Soils are alfisols and ultisols, both with a well-defined argillic horizon and mostly derived from highly-weathered volcanic material (Martínez *et al.* 1993, USDA 1998). Mean annual temperature in these sites is approx. 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, García-Oliva *et al.* 1991).

## PERMANENT PLOTS AND EXPERIMENTAL TREATMENTS

We studied three populations in three different areas within Las Joyas: Site 1 *"El Huiscorol"*, site 2 *"Los Asoleaderos"* and site 3 *"El Zarzamoro"*. All sites are less than one kilometre afar, and located at approximately 19° 36' N and 104° 16' W. All are old maize fields that were abandoned from agriculture in the mid-seventies. 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 (cf. Sarukhán & Harper 1973). In May 1989 we could differentiate the genets that were born in 1988 because they had one or rarely two small shoots, and zero or only one ear. Cohorts born from seed during the five-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, show an acuminate apex. Dead plants were identified by the absence of green shoots and buds, and/or by their disappearance from previously locations. In the first three years, we mapped the plots from May to December at intervals of approximately one month. To describe survivorship curves for cohorts of vegetative shoots, we counted the plants in the plots between January 1992 and November 1993 at intervals of approximately on 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 small one-meter-square plots, we lumped 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 forests). 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 the three treatments to every site (it is especially difficult to apply fire safely during the dry season to only part of a site).

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. Firstly, their management history is comparable, as they were abandoned from cultivation around 1970-1974. 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, there are no more suitable sites than the ones we used. 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 *Zea 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 × 15 cm deep) in January 1990 (immediately after seed masting). We then took five additional samples in November 1990 (after the annual rainy season and before the following masting event). Seed pool was estimated as

$P_{seed} = \dfrac{N_{Nov}}{N_{Jan}} \times 100$, were $N_{Jan}$ is the number of viable seeds found in January (after masting 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 mast), 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.

## SURVIVAL OF GENETS

For the analysis of cohort survival we calculated the time-specific mortality rates, and analysed their relationship with time. By definition, the mortality rate is $\frac{\partial N}{\partial t} = -k_t N$, where $k_t$ is the probability that an individual dies at time $t$. As $\frac{1}{N} \partial N = \partial \log N$, we can rewrite the first equation as $\frac{\partial \log N}{\partial t} = -k_t$. Let us now define $\hat{k}$, the estimated mortality rate, as a difference equation $-\hat{k} = \frac{\Delta \log N}{\Delta t}$. Then for any time $t$, the estimated time-specific mortality rate $\hat{k}_t$ between time $t$ and time $t+x$ can be calculated as $\hat{k} = \frac{\log N_{t+x} - \log N_t}{x}$, where $x$ is the time interval for which the mortality rate was estimated.

With this last equation we calculated mortality rates of the genetic individuals (genets) in each site for each time interval. This method of analysis has the advantage over standard survival curves that each point is truly independent of the previous ones. If the relationship between $\hat{k}$ and $t$ is linear, then $\hat{k} = \beta_0 + \beta_1 t$, where $\beta_0$ is the ordinate at the origin and $\beta_1$ is the slope of the line relating mortality of the cohort to time. If $\beta_1$ does not differ significantly from zero, mortality of the cohort is age-independent. In demographic terms, this means that the survival curve is type II (constant mortality). If $\beta_1$ is significantly greater than zero, mortality increases with cohort age (i.e. the survival curve is type I). If $\beta_1$ is significantly lower than zero, mortality decreases with cohort age ( i.e. the survival curve is type III). Survival was analysed by regression. All data were tested for homoscedasticity, independence and normality of the residual error (Neter *et al.* 1985). We used the General Linear Procedure (GLM) of the SAS statistical package (ver. 6.03; SAS 1988) using a type

III sum of squares. The survival parameters were calculated for all individuals established from seed (i.e. genets) before 1988, in 1988, and in 1989. All cohorts were followed until November 1993.

PRODUCTION AND SURVIVAL OF RAMETS

To analyse the effects of disturbance and years on the production of vegetative stems (ramets) for each genetic individual, we randomly selected 40 individuals from each site and year. Through a Montecarlo process we calculated, for each year, one thousand differences in the number of vegetative shoots between pairs of randomly selected individuals between two sites (selection was done without replacement from a maximum of 1600 pairs). By analysing the differences between sites through time, we removed the fixed effects of the sites and focussed on the site × year interaction. Thus, if the distribution of differences in the number of shoots from one year to the next remained the same, we can conclude that both sites produced vegetative shoots in the same rate as in the previous year. On the other hand, if the distribution that resulted from the Montecarlo simulation changed significantly between years (as shown by a *t*-test), we can conclude that the relative number of vegetative shoots produced in one site had increased or decreased significantly compared to the other site. The significance threshold for the *t*-test was subjected to a Bonferroni correction to allow for multiple non-independent tests.

We only included shoots of individuals that were established at the beginning of our study (i.e. during or before 1988). For the analysis we used the number of vegetative shoots borne by a genet in every year in November (i.e. at the end of the annual reproductive cycle), with the exception of 1992, when we counted the annual shoots in October, as the rainy season that year was one month earlier and the flowering season moved forward correspondingly. We also conducted a survival analysis of vegetative shoots through time following the same methods used to analyse the survival of genets (see above). We analysed

survivorship curves for cohorts of vegetative shoots produced between December 1991 and October 1992 until November 1993.

## PRODUCTION OF EARS AND CARYOPSES

To analyse the effects of site and year on the production of reproductive structures (ears or mature spikes) by each genetic individual or genet, a Montecarlo simulation was used to remove the fixed effect of sites, following the procedure described in the previous section for vegetative shoots. Additionally, to analyse the production of ears in vegetative shoots, we marked all new shoots with differently-coloured plastic labels every month between December 1991 and November 1993. At the end of the reproductive cycle, we counted the number of ears produced by each shoot. For the analysis of ears produced in October 1992, we included all shoots born between December 1991 and October 1992. For the analysis of ears produced in November 1993, we counted ears in all shoots born between October 1992 and October 1993. By means of a contingency-table analysis, we compared the number of ears produced by each monthly cohort against the expected value under the null hypothesis of a uniform distribution (Zar 1984). For the analysis we used the log-linear model in process CATMOD from SAS (1988), and the $G$ statistic was used as a $X^2$ measure of the fit to data (Everitt 1977; Freedman 1987).

### Number of caryopses per ear

In December 1993 we randomly collected fifty-three ears from each site. In the laboratory, we counted the number of seeds (caryopses) in each ear, and then transformed these values to ranks (procedure Rank; SAS 1988). We then analysed the transformed results for between-site differences (procedure GLM; SAS 1988) followed by a SNK multiple-comparison test. Rank transformations provide non-parametric, distribution-free, and robust tests that use standard ANOVA procedures when the untransformed data fail to meet the

parametric requirements of homoscedasticity and normality (Conover & Iman 1981; cited in Seaman *et al.* 1994).

## The effect of fire on the viability of caryopses

Caryopses of *Z. diploperennis* were collected in February 1993, and stored at 0°C. In March of that same year, we placed 50 caryopses in each of fourteen bags made from aluminium mesh (1 mm mesh-size), of size 10 cm × 10 cm. The bags were randomly placed under the stubble of site 3 after slashing the scrub. Subsequently, the site was burned. The bags were collected the following day, and the caryopses were placed in a moist germination chamber (i.e. imbibed in water) for 24 hours at 30°C. Afterwards, the caryopses were bisected and imbibed in tetrazolium chloride solution (0.1% in a pH 7 buffer solution of sodium and potassium phosphate) for three hours at 30°C in a dark chamber. Embryos that turned red were counted as viable (Moreno 1984). The same viability test was performed on six control samples of 50 caryopses which had been kept refrigerated. The proportion of viable seeds in each sample replicate was transformed by an arcsine-square root conversion to improve normality (Zar 1984), and the resulting values were compared between treatments by means of an $F$ test.

## EFFECT OF SIZE AND AGE ON THE FATE OF THE GENET

Some population variables, such as fecundity and mortality, may be affected by age, size or life-cycle stage (Caswell 1989), or by their interactions (Law 1983; Hughes & Connell 1987). Caswell (1986; 1988; in Caswell 1989) developed a log-linear method to evaluate the effect of developmental stages on the demographic fate of the individuals in a population. A multi-way contingency table is constructed relating the age ($A$), size ($S$), and fate ($F$) of the genet. The entry $m_{ijk}$ in cell ($ijk$) of the table gives the number of individuals starting in age $i$ and size $j$ at time $t$ and achieving fate $k$ at time $t+1$. This table can be analysed as a log-linear model with $X^2$ goodness of fit (Everitt 1977). A model is first fitted including all the main

effects of size, age, and fate, as well as the interaction term ($S \times A$). The effect of size on the fate of the genet is then explored by adding the interaction term ($S \times F$) and evaluating its significance. Similarly, the effect of age is explored through the interaction term ($A \times F$), and, lastly, the possibility that age and size may have a synergistic effect on genet fate is explored through the three-way interaction term ($S \times A \times F$). We used three size categories (genets without flowering shoots, genets with 1-2 flowering shoots, genets with 3 or more flowering shoots), four age categories (1, 2, 3, and 4 or more years old), and three fate categories (flowering, vegetative, dead).

## 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 1-2 flowering shoots, and (d) genets with 3 or more flowering shoots (Fig.1). The population growth rate ($\lambda$, 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 (Caswell 1989). To eliminate the fixed effect of sites, we subtracted for each $\lambda$-value in each site the value of $\lambda$ 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 4 yearly growth rates (in which the fixed effect of sites may bias our statistical analysis) into a new series of 3 deviations from the value in these year (from which the fixed effect of the site had been removed). Inter-site comparisons were made on the transformed series.

### Loop analysis

A more 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). The method consisted of four basic steps, as described by Wardle

(1998): (1) We constructed a life-cycle graph and population transition matrix of the *Zea diploperennis* population. (2) We calculated the elasticity values of the matrix according to Caswell (1989). (3) We decomposed the life cycle graph into unbranched loops in such a way that all transitions were incorporated at least once into some loop, using software developed by van Groenendael *et al.* (1994). The characteristic elasticity of the loop was estimated as the elasticity of the transition element that is unique to the loop. (4) The loop elasticity was calculated by multiplying the characteristic elasticity by the number of transition elements within the loop.

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 alternative loop to the population growth rate $\lambda$. We classified all the possible loops in the *Zea 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 group of loops to $\lambda$, we could estimate the contributions of persistence, sexual reproduction, and vegetative growth to population dynamics.

Simulation analyses

One widely use method for exploring the consequences of different management scenarios is to project the population transition matrices following pre-defined rules (see 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 detect the frequency of disturbance regimes that favour persistence of *Zea diploperennis*. 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 10 years to the demographic projections, a 1/7 scenario with disturbance every seven years, 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 perturbation was applied, and the 1992-93 matrix to simulate experimental perturbation. In the case of site 1, no perturbation treatment was ever applied, the alternating between years served as a statistical control to verify that the observed trends were not an artefact of the transition probabilities of a given year.

## 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). To simulate slash-and-burn disturbance, we further decreased the slash probability of permanence, taking into account that only 11.7% of the burned caryopses survived (see below), to produce a value of 0.04.

### POPULATION FLOWS AND SURVIVAL OF GENETS

Two periods of high birth rate were observed during the springs of 1989 and 1991, followed by two events of accelerated mortality in the summer and fall of the same two years. In the other years (1990, 1992 and 1993) the peak of spring births was much lower, or even undetectable, and the peak of summer deaths was also negligible (Fig.2). 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).

A similar trend was observed in the survivorship curves of genets at all three sites (Table 1 and Fig.2): The curves for the pre-1988 cohort approached a type-II curve, with constant and relatively low mortality rates of around 0.02 month$^{-1}$; the 1989 cohort showed a marked type-III curve with very high initial mortalities (around 0.1-0.2 month$^{-1}$) that decreased to around 0.07-0.09 (still a high value compared to the pre-1988 cohort) after two years, and the 1988 cohort showed intermediate survival values and an intermediate shape, with a type-II mortality pattern in sites 1 and 2, and a low-curvature type-III pattern in site 3.

56

All later cohorts (from 1990 to 1993) showed too few established individuals to make any statistical tests on their mortality rates, and also died off very quickly, within periods ranging from one to six 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. 3, 294; $p < 0.0001)$ and a significant interaction term was also found between time and cohorts $(F = 9.65$; d.f. 3, 294; $p < 0.0001)$, but no significant differences were attributable to the effect of either the site or the type of disturbance.

The age-structure of the genets at the end of each growth cycle (i.e. in October-November) for years 1 to 5 was relatively similar in the three sites. The pre-1988 cohort was proportionally more abundant at the end of the study (November 1993) in all sites. Also there was no successful recruitment from the 1990-1992 cohorts (a period without disturbances) in any of the three sites, except for one individual from the 1991 cohort that survived in site 1. The 1988 cohort died on average more rapidly in site 1 than in the other sites.

PRODUCTION AND SURVIVAL OF RAMETS

The Montecarlo simulation evaluating the statistical distribution of inter-site randomised differences showed that these distributions did not differ between 1989, 1990, and 1993. That is, during these years the fixed effects determining differences between sites remained relatively constant. In years 1991 and 1993, however, the distribution of inter-site differences changed significantly. These years correspond to the times when experimental disturbances were applied.

The total number of non-reproductive ramets tended consistently to decrease with time in all three sites (see Fig.3). Flowering shoots, however, showed a trend that differed between sites, as discussed in the previous paragraph. While flowering ramets tended to decrease in the undisturbed site 1, they showed marked increases in sites 2 and 3, especially

in years 1991 and 1993, after the disturbance treatments were applied (Fig.3b). As would be expected, those high-disturbance events were also followed by a marked increase in the production of ears and caryopses (Fig.3c).

Most of the shoots produced between December 1991 and August 1992 had produced reproductive structures (ears) by October 1992, started to die-off during the dry season of 1992-93, and were all dead by June 1993 when the following rainy season started (Fig.4). The shoots produced during, or after, September 1992 did not reproduce that year, and some managed to survive until the next fruiting season in October 1993. The survival analysis was made only for those cohorts that completed their growth cycle, i.e. for the vegetative cohorts produced between December 1991 and October 1992. In all three sites, mortalities did not change significantly with time (the slope tests for the mortality *vs.* time regression curve gave $p$-values higher than 0.06 for all cohorts in site 1, higher than 0.07 for all cohorts in site 2, and higher than 0.10 for all cohorts in site 3).

## PRODUCTION OF EARS AND CARYOPSES

As for clonal shoots, the Montecarlo simulation evaluating the statistical distribution of inter-site randomised differences showed no differences between 1989 and 1990. During these two years the effects determining fixed differences between sites remained relatively constant. In years 1991 and 1993, however, the distribution of inter-site differences changed significantly. These years correspond to the experimental disturbances. Finally, in year 1992, sites 1 and 2 did not show significant differences but the differences involving site 3 (s1-s3 and s2-s3) changed significantly. The results suggest that the disturbance treatments had a significant effect on the production of ears and caryopses, independently of the fixed effects that may be ascribed to each site. Additionally, the results suggest that in site 3 the increased fertility caused by disturbance in 1991 spilled over into year 1992 (see Fig.3c).

In general, the production of ears in site 1 tended to decrease consistently with time, while in sites 2 and 3 it tended to increase (Fig.3a). This increase was especially high in years after the sites were subject to disturbances. Disturbance seemed to especially 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; $p < 0.00001$).

In the two reproductive cycles (1992 and 1993) in which we distinguished the contributions of the monthly cohorts of ramets to the production of ears (Fig.5), we found significant differences between cohorts ($G = 929.4$; d.f. 9; $p < 0.00001$) and between sites ($G = 340.5$; d.f. 3; $p < 0.00001$). The interaction between cohorts and sites was also significant ($G = 416.59$; d.f. 16; $p < 0.00001$). In October 1992, the cohorts producing more ears were those derived from ramets born during the dry season (January to May 1992). In site 3, the January cohort was the one that produced more ears, while in sites 1 and 2 it was the May cohort. In November 1993, however, there was a marked shift in the success of the monthly cohorts of ramets. The cohorts producing more ears in all sites were those derived from ramets produced towards the end of the dry season (June 1993).

Significant differences were observed between sites in the number of caryopses produced per ear ($F = 3.99$; d.f. = 2,155; $p = 0.02$). Reproductive shoots at site 1 produced significantly fewer caryopses per ear ($6.35 \pm 0.16$) than those at sites 2 and 3 ($7.08 \pm 0.22$, and $6.92 \pm 0.19$, respectively), which in turn did not differ significantly in caryopsis production. Finally, highly significant differences were also found in the percentage of viable embryos between the caryopses in the control treatment ($85.7 \pm 2.16\%$) and those produced in the fire treatment ($11.7 \pm 6.28\%$) in site 3 ($F = 60.9$; d.f. = 1,18; $p < 0.001$).

EFFECT OF SIZE AND AGE ON THE FATE OF THE GENET

We found that both age and size had a strong and significant influence on the fate of the genet in all three sites (Table 2). The log-linear estimates indicate that smaller plants are more

frequently non-flowering and that they die with a higher frequency than the larger plants. A similar result was observed for age. As a general rule, older plants had a lower probability of death, and it was also unlikely that they would revert to a non-flowering state. No significant interactions were found between age and size in relation to fate. Additionally, the log-linear model showed that the two predictors (age and size) are themselves significantly related; older plants tend to be larger.

## PROJECTION MATRIX MODELS

The population growth rates of the genets were negative in all three sites at the beginning of the observations (1989; Table 3). After that first year, however, when the disturbance treatments were applied, the values of $\lambda$ increased in the disturbed sites 2 and 3, but increased less in the undisturbed site 1. When the series of $\lambda$-values was transformed into deviations from the base year (1989), it was found 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, $\lambda$ achieved values higher than unity in the two years in which perturbation was applied (90-91 and 92-93), and in site 3, $\lambda$ was higher than unity after slash-and burn was applied (92-93). In site 1, in contrast, genet growth rates were consistently lower than unity.

### 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.6). 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.7). Additionally, it was found that the mean elasticity of the sexual reproduction loops was significantly lower than those for the persistence and the vegetative growth loops ($x = 5.8 \pm 4.3$, $28.4 \pm 6.5$, and $8.2 \pm 7.1$, respectively).

## Simulation analysis

The projection of population transition probabilities for the genets in site 1 (undisturbed) showed that, 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.8). 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 two years (simulation with transition data from years 1989-90 and 1990-91), or once every three years (simulation with transition data from years 1991-92 and 1992-93). 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 was 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.

## Discussion

### EXPERIMENTAL TREATMENTS

The effects of disturbances such as slash and burn have been an important subject in plant population dynamics (Loucks *et al.* 1985; Silva *et al.* 1991; Joy 1992; Whelan 1995). Few of these studies, however, have been done on plants of extreme rarity such as *Zea diploperennis*. Rare species with extremely patchy distributions, such as this one, present restrictions for experimental work as proper replication cannot be achieved. In spite of this major shortcoming, the challenges imposed by extremely rare and endangered species must be met if their conservation is to be achieved. This is especially true in the case of *Zea 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 contributed to reduce the pseudo-replication effect of repeated measures (Mead 1990).

### SURVIVAL OF GENETS

The effect of disturbance on genets was not marked; both the establishment and the mortality patterns were qualitatively similar in the three sites. The pre-1988 and the 1988 cohorts approached a type-II survivorship curve, while the 1989 cohort showed a more marked type-III curve. However, the 1989 cohort was followed since establishment while the previous cohorts were recorded from a later time. It is likely that initial mortality was high in all cohorts, tending to approach a stable lower value later in life. High initial mortalities during establishment tending to level-off as the seedlings mature have been described for other plant species (e.g. Harper 1977, Sarukhán and Harper 1973, Hutchings and Bradbury 1986). As *Z. diploperennis* cohorts age, mortality decreases, eventually reaching a stable rate

for adult individuals. This was observed in all three sites, including those that were slashed or slashed-and-burned. The experimental disturbances did not change the patterns of recruitment, establishment and mortality of genets compared with the undisturbed site.

The age structures of the three populations of *Z. diploperennis* were dominated by three age 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, additionally, the presence of adults does not necessarily mean that the site is favourable for seedlings (Kays & Harper 1974; Williams 1975; Lovett-Doust 1981; Eriksson 1988, 1993; Maddox *et al.* 1989; Aguilera & Lauenroth 1993; Sánchez-Velásquez *et al.* in press). It is not rare to find clonal populations of plants consisting of only one or two, numerically large, age classes (Crawley 1990). 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).

PRODUCTION AND SURVIVAL OF RAMETS

In sharp contrast with the demography of genets, disturbances had a significant effect on the number of ramets. In site 1 the number of vegetative shoots decreased with time, whereas in the other sites it increased or remain constant. The increase in vegetative shoots was most conspicuous in site 3 during 1993, after the slash-and-burn treatment. These results suggest that the main consequence of disturbance is to promote active vegetative propagation of genets through rhizome growth and production of aerial shoots (Sánchez-Velásquez *et al.* 1992); similar responses to disturbance have been observed in other grass species (Silva *et al.* 1991; Joy 1992). It has also been reported for other species that disturbance may promote clonal growth and that burning may help to maintain grasslands (see Loucks *et al.* 1985; Hughes *et al.* 1991; West 1993). In addition to the effect of disturbance, the highest

production of clonal shoots was coincident with the rainy season (May to October; see Fig.4), a pattern common in other clonal species (Abrahamson 1980).

Hartnett & Bazzaz (1985) have suggested that many clonal perennial species with connected modules exhibit a constant mortality pattern through time, i.e. a type-II mortality pattern. The survival curves of ramets of *Z. diploperennis* showed a type-II mortality pattern. A similar demographic pattern was observed in *Aphelandra aurantica*, a tropical herbaceous perennial species (Calvo 1989; cited in Martínez-Ramos & Álvarez-Buylla 1995).

SEED POOL AND PRODUCTION OF CARYOPSES

Mast seeding is the synchronous production of seed at long intervals by a population of plants (Janzen 1976). Eight hypotheses have been suggested as mechanisms favouring mast seeding (Kelly 1994). In the case of *Z. diploperennis*, massive production of seeds was observed in our sites after disturbance, especially after burning. This behaviour is in agreement with Kelly's "resource matching" hypothesis, i.e. mast seeding seems to be a response to pulses of disturbance, which potentially provide new resources and new spaces for establishment. Additionally, mast seeding counters the mortality that fires may bring upon the seed bank in the soil, which according to our results may reduce the number of viable seeds by more than 80%. 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). Fire has been for centuries an important management tool for indigenous farmers in Manantlán, and has hence been an important element in the past demography of *Zea diploperennis* (Benz *et al.* 1990; Sánchez-Velásquez 1991), while cattle have been one of the main dispersal agents of the plant's propagules (Iltis 1980; Benz et al 1990; Guzmán and Iltis 1991). *Z. diploperennis* seems to be highly tolerant to these disturbances.

Within the 1992 and 1993 shoot cohorts, the ones that produced more ears were those generated in early spring 1992 and in summer 1993. It is interesting to note that 1992 was an anomalous year, with winter and spring rains, while 1993 had normal summer rains. Thus, ramets growing in rainy months yield more fertile ears.

## EFFECT OF SIZE AND AGE ON THE FATE OF THE GENET

Some studies have demonstrated that for many plants size is more strongly associated with population parameters than age (e.g., Hughes 1984; Eriksson 1989; Hara 1988; Lomnicki 1988; Caswell 1989; Silva *et al.* 1991; Svensson *et al.* 1993; Bengtsson 1993; Olmsted & Álvarez-Buylla 1995). In this study, however, we found that age and size are correlated, and that both affect the final fate of the genet. Knowing that in any rare population size is as good or better a predictor of genet fate than age is relevant to make decisions for the conservation and management of the population, as size is easier to measure in the field than age.

## PROJECTION MATRIX MODELS

In the absence of disturbance, population growth tends to be negative ($\lambda < 1$). Experimental disturbance increased the production of seeds enough to produce a significant increase in the growth rates of the genets. Although slashing of the successional scrub produced an increase in the values of $\lambda$, 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 genet demography from negative to positive growth. Silva *et al.* (1991) found similar dramatic increases in the population growth rates of the grass *Andropogon semiberbis* when burning was applied.

Loop analysis showed that in almost all situations, with or without disturbance, persistence is the most important life-history pathway of *Zea diploperennis* in relation to its relative contribution to fitness (Fig.6). Although, quantitatively, sexual growth loops contribute

less to the species' fitness, bouts of seed production and subsequent germination are the major

causes of positive 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

simulated growth of the population of genets become positive.

FIRE AND CONSERVATION OF *Z. DIPLOPERENNIS*

Fire is an important factor for the evolution and maintenance of many plant species,

especially in fire-prone grasslands (West 1993) and conifer forests (Cottan 1981; Heinselman

1981). The effect of fires on a given population will depend on the frequency, intensity and

periodicity of burning (see White 1979; Pickett & White 1985). The growth of grass species

can be positively affected by fire (Joy 1992). The fact that the demography of genets in *Zea*

*diploperennis* is not affected by disturbance, and that the production of ramets 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 of high risk, 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 the Sierra de Manantlán Biosphere Reserve for many years, and have adversely affected the

montane forests (Jardel 1991, Sánchez-Velásquez *et al.* 1996). 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.

CONCLUSIONS

Our study demonstrates that the populations of *Zea diploperennis* respond positively to

slash, and slash-and-burn. Disturbances affect the population at both the levels of ramet and

genet demography. At the level of the individual ramets, disturbances dramatically enhanced the number of vegetative shoots within each genet and the number of shoots with reproductive ears. Thus, in the year following a disturbance there is an increased rain of seeds into the soil seed bank, followed by a bout of germination. At the level of genet demography, increased germination leads to the establishment of new genets in the population. Because of the marked type-III survivorship curve of seedlings, most of the new recruits will die, but a few may survive and help to maintain, or even increase, the number of genets.

Without any disturbance, the net recruitment of new genetic individuals into the three populations of *Z. diploperennis* in the core area of Las Joyas is almost zero. Experimental disturbances promote vigorous vegetative growth and massive seed production. The number of genetic individuals in the three sites within Las Joyas is gradually decreasing without disturbance, and if the trend continues, the populations may face severe genetic impoverishment and even local extinction within the core area of the reserve. It is ironic that the plant that gave origin to the conservation programme seems to be doing worse in the core area than in the peripheral buffer zones, where indigenous agriculture is still performed. Although we have not analysed in this study the fate of newly established genets in recently slashed and burned forests, simple descriptive observations suggest that the opening of new areas promotes the establishment of new genets.

The best way to preserve the species seems to be through the management of the whole population in a similar manner to traditional itinerant slash-and-burn agriculture. Instead of applying recurrent disturbances to patches where populations are already found, a program should be established to itinerantly sow *Z. diploperennis* in new, recently disturbed areas, trying to simulate in this manner the type of "fugitive," highly disturbed environments to which the species is so clearly adapted. Studies of genetic diversity in the protected populations of Las Joyas compared to the populations in the buffer area under traditional

indigenous use may also bring new and important elements for the successful conservation of *Zea diploperennis*.

## Acknowledgements

# References

Abrahamson, W. G. (1980). Demography and vegetative reproduction. *Demography and evolution in plant populations*. (ed. O. T. Solbrig), pp 89-106. Blackwell Scientific Publications, Oxford.

Aguilera, M.O. & Lauenroth, W.K. (1993). Seedling establishment in adult neighborhoods - intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. *Journal of Ecology*, **81**, 253-261.

Bengtsson, K. (1993). *Fumana procumbens* on Öland – population dynamics of a disjunct species at the northern limit of its range. *Journal of Ecology*, **81**, 745-758.

Benz, B.F., Sánchez-Velásquez, L.R. & Santana-Michel, F. (1990). Ecology and ethnobotany of *Zea diploperennis*: Preliminary investigations. *Maydica*, **35**, 85-98.

Brussard, P.F. (1991). The role of ecology in biological conservation. *Ecological Applications*, **1**, 6-12.

Caswell, H. (1989). *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer, Massachusetts.

Cottam, G. (1981). Patterns of succession in different forest ecosystems. *Forest Succession: Concepts and Application*. (eds. D. C. West, H. H. Shugart & D. B. Botkin), pp. 178-184. Springer-Verlag, New York.

Crawley, M.J. 1990. The population dynamics of plants. *Philosophical Transactions of the Royal Society of London*, **330**, 125-140.

Ehrlén, J. & van Groenendael, J. (1997). Direct disturbance analysis for better conservation. *Conservation Biology*, **12**, 470-474.

Eriksson, O. (1988). Ramet behaviour and population growth in the clonal herb *Potentilla anserina*. *Journal of Ecology*, **76**, 522-536.

Eriksson, O. (1989). Seedling-dynamics and life histories in clonal plants. *Oikos*, **55**, 231-238.

Eriksson, O. (1993). Dynamics of genets in clonal plants. *Trends in Ecology and Evolution*, **8**, 313-316.

Everitt, B.S. (1977). *The analysis of contingency tables*. John Wiley & Sons, Inc., New York.

Excel (ver. 1997). Microsoft Corporation. USA.

FAO. (1989). *Recursos fitogenéticos, su conservación in situ para el uso humano*. Organización de las Naciones Unidas para la Agricultura y la Alimentación, Roma, Italy.

Freedman, G. (1987). *Applied Categorical Data Analysis*. Marcel Dekker, Inc. New York.

García-Oliva, F., E. Ezcurra and L. Galicia. 1991. Patterns of rainfall distribution in the Central Pacific Coast of Mexico. *Geografiska Annaler*, **73**, 179-186.

Guzmán, R., & Iltis, H.H. (1991). Protección a genes perennes de maíz en una reserva de la biosfera. *Diversity*, **7**, 89-92.

Hara, T. (1988). Dynamics of size structure in plant populations. *Trends in Ecology and Evolution*, **3**, 129-132.

Hartnett, D.C., & Bazzaz, F.A. (1985). The genet and ramet population dynamics of *Solidago canadensis* in an abandoned field. *Journal of Ecology*, **73**, 407-413.

Harper, J.L. (1977). *Population Biology of Plants*. Academic Press, London.

Harper, J.L. (1985). Modules, branches, and the capture of resources. *Population Biology and Evolution of Clonal Organisms* (eds. J. B. C. Jackson, L. W. Buss & R. E. Cook), pp. 1-30. Yale University Press, New Haven.

Harvey, H.J. (1985). Population biology and the conservation of rare species. *Studies in Plant Demography* (ed. J. White), pp. 111-123. Academic Press, London.

Heinselman, M.L. (1981). Fire and succession in the conifer forest of northern north America. *Forest Succession: Concepts and Application*. (eds. D. C. West, H. H. Shugart & D. B. Botkin), pp. 374-405. Springer-Verlag, New York.

Hernández-Vargas, G., L. R. Sánchez-Velásquez, T. Carmona V., Ma. del R. Pineda L. & R. Cuevas G. (2000). Efecto de la ganadería extensiva sobre la regeneración arbórea de los bosques subtropicales de montaña en la Sierra de Manantlán. *Madera y Bosques*, **6**, 13-28.

Howe, H.F. (1995). Succession and fire season in experimental prairie plantings. *Ecology*, **76**, 1917-1925.

Hughes, T.P. (1984). Population dynamics based on individual size rather than age: A general model with a reef coral example. *The American Naturalist*, **123**, 778-795.

Hughes, T.P. & Connell, J.H. (1987). Population dynamics based on size or age? A reef-coral analysis. *The American Naturalist*, **129**, 818-829.

Hughes, T.P., Vitousek, P.M. & Tunison, T. (1991). Alien grass invasion and fire in the seasonal submontane zone of Hawaii. *Ecology*, **72**, 743-746.

Hutchings, M. & Bradbury,I.K. (1986). Ecological perspectives on clonal perennial herbs. *BioScience*, **36**, 178-182.

Iltis, H.H., Doebley, J.F., Guzmán, M, R. & Pazy, B. (1979). *Zea diploperennis* (Gramineae): A new teosinte from Mexico. *Science*, **203**, 186-188.

Iltis, H.H. (1980). The 3rd University of Wisconsin-University of Guadalajara teosinte expedition to the Sierra de Manantlán, Jalisco, Mexico: December 28, 1979 to January 21 1980. Background, preliminary results and commentary on nature preservation in Mexico. (Reissued with corrections as Contributions from the University of Wisconsin Herbarium 1, December 1983).

Iltis, H.H. (1993). La taxonomía del *Zea* desde una perspectiva histórica. *Biología, Ecología y Conservación del Género Zea* (ed. B. F. Benz), pp. 17-41. Universidad de Guadalajara, Guadalajara, Jalisco, México.

Janzen, D.H. (1976). Why bamboos wait so long to flower. *Annual Review Ecology and Systematics*, **7**, 347-391.

Jardel, P.E.J. (1991). Perturbaciones naturales y antropogénicas y su influencia en la dinámica sucesional de los bosques de Las Joyas, Sierra de Manantlán, Jalisco. *Tiempos de Ciencia*, **22**, 9-26.

Jardel, P.E.J. (1992). *Estrategia para la Conservación de la Reserva de la Biosfera Sierra de Manantlán*. Universidad de Guadalajara, Guadalajara, Jalisco, México.

Joy, B. (1992). Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science*, **3**, 187-200.

Kays, S. & Harper, J. (1974). The regulation of plant and tiller density in a grass sward. *Journal of Ecology*, **62**, 97-105.

Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution*, **9**, 465-470.

Law, R. (1983). A model for the dynamics of a plant population containing individuals classified by age and size. *Ecology*, **64**, 224-230.

Lesica, P. (1992). Autoecology of the endangered plant *Howellia aquiatilis*; implications for management and reserve design. *Ecological Applications*, **2**, 411-421.

Lomnicki, A. (1988). *Population Ecology of Individuals*. Monographs in Population Biology No. 25. Princeton University Press, New Jersey.

Lorente-Adame, R. G., & Sánchez-Velásquez, L.R. (1996). Dinámica estacional del banco de frutos del teocintle *Zea diploperennis* (Gramineae). *Biotropica*, **28**, 267-272.

Loucks, O. L., Plumb-Mentjes, M.L. & Rogers, D. (1985). Gap processes and large-scale disturbances in sand prairies. *The Ecology of Natural Disturbance and Patch Dynamics* (eds. S. T. A. Pickett & P. S. White), pp. 72-83. Academic Press, San Diego.

Lovett Doust, L. (1981). Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*): I. The dynamics of ramet in contrasting habitats. *Journal of Ecology*, **69**, 743-755.

Maddox, G. D., Cook, R. E., Winberger, P.H. & Gardescu, S. (1989). Clone structure in *Solidago altissima* (Asteraceae) populations: Rhizome connections within genotypes. *American Journal of Botany*, 76, 318-326.

Martínez-Ramos, M. & Álvarez-Buylla, E. (1995). Ecología de poblaciones de plantas en una selva húmeda de México. *Boletín de la Sociedad Botánica de México*, 56, 121-153.

Martínez, R.L.M., J.J. Sandoval L. & R.D. Guevara G. (1991). El clima de la Reserva de la Biosfera Sierra de Manantlán (Jalisco-Colima, México) y su área de influencia. *Agrociencia: Serie Agua-Suelo-Clima*, 2, 107-119.

Martínez, R.L.M., I.R. Delgado & R.I. Flores. (1993). Suelos de la Estación Científica Las Joyas, Reserva de la Biosfera Sierra de Manantlán, Jalisco. *Agrociencia: Serie Agua-Suelo-Clima*, 3, 103-115.

Mead, R. 1990. *The Design of Experiments: Statistical Principles for Practical Applications*. Cambridge University Press.

Moreno, E. M. (1984). *Análisis Físicos y Biológicos de Semillas Agrícolas*. Instituto de Biología, Universidad Nacional Autónoma de México. México, D. F.

Neter, J., Wasserman, W. & Kutner, M.H. 1985. *Applied Linear Statistical Models*. Second edition. Richard D. Irwin, Inc., Homewood, Illinois.

Olmsted I. & Álvarez-Buylla, E. (1995). Sustainable harvesting of tropical trees: Demography and matrix models of two palm species in Mexico. *Ecological Applications*, 5, 484-500.

Owen, W. R. & Rosentreter, R. (1992). Monitoring rare perennial plants: Techniques for demographic studies. *Natural Areas Journal*, 12, 32-38.

Pickett, S. T. A. & White, P.S. (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press Inc., San Diego.

Pineda-López, Ma. del R. (1988). *Efecto de las perturbaciones en la estructura y composición de los bosques templados de Las Joyas, Sierra de Manantlán*. M. Sc. Thesis, Instituto Nacional de Investigaciones sobre Recursos Bióticos. Xalapa, Veracruz, México.

Rabinowitz, D., Cairs, S. & Dillon, T. (1986). Seven forms of rarity and their frequency in the flora of the British Isles. *Conservation Biology* (ed. M. E. Soulé), pp. 182-204. Sinauer Associates Inc., Massachusetts.

Saldaña, A.A., & Jardel, E.J. 1992. Regeneración natural del estrato arbóreo en bosques subtropicales de montaña en la Sierra de Manantlán, México: Estudios preliminares. *Biotam*, **4**, 36-50.

Sánchez G. J. & Ordaz, S.L. (1987). *El Teocintle en México: Distribución y Situación Actual de las Poblaciones*. Systematic and Ecogeographic Studies on Crop Genepools No. 2, IBPGR. Rome, Italy.

Sánchez-Velásquez, L. R. (1988). *Sucesión forestal en la Sierra de Manantlán, Jal., México*. M.Sc. Thesis, Centro de Botánica, Colegio de Posgraduados, Texcoco estado de México, México.

Sánchez-Velásquez, L.R. (1991). *Zea diploperennis*: Mejoramiento genético del maíz, ecología y la conservación de recursos naturales. *Tiempos de Ciencia*, **24**, 1-8.

Sánchez-Velásquez, L.R., Solís-M., A., Cortez, E., Jiménez, R.G., Rosales, M.P & Cárdenas, A. (1992). Efecto del cultivo tradicional del maíz sobre el crecimiento y desarrollo de *Zea diploperennis*. *Biotam*, **3**, 51-58.

Sánchez-Velásquez, L.R. & García-Moya, E. (1993). Sucesión forestal en la Sierra de Manantlán Jal., México: Bosque mesófilo de montaña y bosque de *Pinus*. *Agrociencia*, **3**, 7-26.

Sánchez-Velásquez, L.R., R.G. Jiménez, G. & B.F. Benz. (In press). Population dynamics and ecology of a rhizomatous species of teosinte *Zea diploperennis*: I. Population flux of modules and genets. *Revista de Biología Tropical*, 48.

Sánchez-Velásquez, L.R., Rosales, A.J.J., Pineda-López, Ma. del R. & Saldaña, A. Ma. de los A. (1996). Descripción cuantitativa de la vegetación de la Estación Científica Las Joyas, Sierra de Manantlán, Jal., México. *Boletín del Instituto de Botánica de la Universidad de Guadalajara*, 4, 73-156.

Sarukhán, J. & Harper, J.L. (1973). Studies in plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L.: I. Population flux and survivorship. *Journal of Ecology*, 61, 676-716.

SAS. (1988). *SAS/STAT User's Guide: Release 6.03 edition*. SAS Institute, Cary, North Carolina.

Seaman, J.W.Jr., Walls, S.C., Wise, S.E. & Jaeger, R.G. (1994). Caveat emptor: Rank transform methods and interaction. *Trends in Ecology and Evolution*, 9, 261-263.

Silva, J. E., Raventos, J., Caswell, H. & Trevisan, M.C. (1991). Population responses to fire in a tropical savanna grass, *Andropogon semiberbis*: A matrix model approach. *Journal of Ecology*, 79, 345-356.

Svensson, B. M., Carlsson, B.Å., Karlsson, P.S. & Nordell, O. (1993). Comparative long-term demography of three species of *Pinguicula*. *Journal of Ecology*, 81, 635-645.

Tuljapurkar, S. & Caswell, H. (eds.) (1997). *Structured-population Models in Marine, Terrestrial, and Freshwater Systems*. Chapman & Hall. NY.

USDA. 1998. *Keys to soil taxonomy, Unites States Department of Agriculture, Natural Resources Conservation Service*. USA.

van Groenendael, J., de Kroon, H. & Tuljapurkar, S. (1994). Loop analysis: Evaluating life history pathways in population projection matrices. *Ecology*, 75, 2410-2415.

Vázquez, G.A. & Cuevas-G., R. (1995). Diversidad, estado, usos y conservación de la flora vascular de la Sierra de Manantlán. *Flora de Manantlán* (eds. A. Vázquez, R. Cuevas, T. S. Cochrane, H. H. Iltis, F. Santana, & L. Guzmán), pp. 61-71. Sida, Botanical Miscellany No. 13, Botanical Research Institute of Texas.

Wardle, G. M. (1998). A graph theory approach to demographic loop analysis. *Ecology*, 79, 2539-2549.

Watson, L.E., Uno, G.E., McCarty, N.A. & Kornkven, A.B. (1994). Conservation biology of a rare species, *Eriocaulon kornickianum* (Eriocaulaceae). *American Journal of Botany*, 82, 980-986.

Weaver S.E. & Cavers, P.B. (1980). Reproductive effort of two perennial weed species in different habitats. *Journal of Applied Ecology*, 17, 505-513.

Wellhausen, E.J., Roberts, L.M. Hernández, X. E, & Mangelsdorf, P.C. (1951). *Razas de maíz en México: Su origen, características y distribución*. Folleto Técnico No. 5, Oficina de Estudios Especiales, Secretaría de Agricultura y Ganadería, México D. F.

West, N.E. (1993). Biodiversity of rangelands. *Journal of Range Management*, 46, 2-13.

Whelan, R.J. 1995. *The Ecology of Fire*. Cambridge Studies in Ecology. Cambridge University Press.

White, D.C. (1979). Pattern, process, and natural disturbance in vegetation. *Botanical Review*, 45, 229-299.

Williams, G.C. (1975). *Sex and Evolution*. Princeton University Press, Princeton.

Zar, J.H. (1984). *Biostatistical Analysis*. Prince Hall, Englewood Cliffs, New Jersey.

Table 1. Relationship between mortality rate and time as indicated by a linear regression. The curve type is indicated by the slope (*ns* indicates a non-significant linear relationship). The values in parentheses are standard errors. In the cases in which mortality did not change significantly with time, the value given for mortality at $t=0$ is the mean value for the whole time series (indicated by an asterisk).

| Site | Cohort | Mortality at $\underline{t}=0$ | Slope | $p$ | Curve type |
|------|--------|---------|-------|-----|------------|
| 1 | <1988 | 0.025 (0.005)* | - | *ns* | type II |
| 1 | 1988 | 0.065 (0.002)* | - | *ns* | type II |
| 1 | 1989 | 0.134 (0.029) | -0.0024 (0.0009) | 0.014 | type III |
| 2 | <1988 | 0.0131 (0.003)* | - | *ns* | type II |
| 2 | 1988 | 0.031 (0.006)* | - | *ns* | type II |
| 2 | 1989 | 0.115 (0.026) | -0.0023 (0.0008) | 0.001 | type III |
| 3 | <1988 | 0.028 (0.006) | -0.0005 (0.0002) | 0.012 | type III |
| 3 | 1988 | 0.103 (0.017) | -0.0024 (0.0005) | 0.001 | type III |
| 3 | 1989 | 0.223 (0.034) | -0.0053 (0.0011) | 0.001 | type III |

Table 2. Log-linear analysis of the effect of size ($S$; represented by different size-classes, $i.\ e.$, vegetative stems, 1-2 flowering stems, and $\geq 3$ flowering stems), age ($A$; 1, 2 , 3, and $\geq 4$ years old), and fate ($F$; flowering, vegetative, dormant, or dead) of *Zea diploperennis* in three sites with different management in the Sierra de Manantlán, Mexico. Hierarchical model was conveniently specified, *e.g.*, the model AS, F contains the terms A, S, F, and AS.

| Model | Site 1 | | | Site 2 | | | Site 3 | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | d.f. | $G^2$ | $P$ | d.f. | $G^2$ | $P$ | d.f. | $G^2$ | $P$ | d.f. | $G^2$ | $P$ |
| AS, F | 13 | 107.39 | | 11 | 122.24 | | 10 | 266.17 | | 15 | 506.58 | |
| AS, SF | 9 | 27.11 | | 7 | 90.44 | | 7 | 195.56 | | 11 | 267.11 | |
| SF | 4 | 80.28 | < 0.001 | 4 | 31.8 | < 0.001 | 3 | 70.61 | < 0.001 | 4 | 239.47 | < 0.001 |
| | | | | | | | | | | | | |
| AS, F | 13 | 107.39 | | 11 | 122.24 | | 10 | 266.17 | | 15 | 506.58 | |
| AS, AF | 8 | 45.29 | | 6 | 26.77 | | 5 | 16.00 | | 10 | 120.26 | |
| AF | 4 | 62.1 | < 0.001 | 5 | 95.47 | < 0.001 | 5 | 250.17 | < 0.001 | 5 | 386.32 | < 0.001 |
| | | | | | | | | | | | | |
| AS, AF | 8 | 45.29 | | 6 | 26.77 | | 5 | 16.00 | | 10 | 120.58 | |
| AS, SF,AF | 4 | 3.19 | | 2 | 3.84 | | 2 | 0.70 | | 6 | 11.63 | |
| SF | 4 | 42.1 | < 0.001 | 4 | 22.93 | < 0.001 | 3 | 15.3 | < 0.001 | 4 | 108.95 | < 0.001 |
| | | | | | | | | | | | | |
| AS, SF | 9 | 27.11 | | 7 | 90.44 | | 7 | 195.56 | | 11 | 267.11 | |
| AS, SF, AF | 4 | 3.19 | | 2 | 3.84 | | 2 | 0.70 | | 6 | 11.63 | |
| AF | 5 | 23.92 | < 0.001 | 5 | 86.6 | < 0.001 | 5 | 194.3 | < 0.001 | 5 | 255.48 | < 0.001 |
| | | | | | | | | | | | | |
| AS, SF, AF | 4 | 3.19 | | 2 | 3.84 | | 2 | 0.70 | | 6 | 11.63 | |
| ASF | 0 | 0 | | 0 | 0 | | 0 | 0 | | 0 | 0 | |
| ASF | 4 | 3.19 | < 0.527 | 2 | 3.84 | 0.147 | 2 | 0.70 | 0.705 | 9 | 11.63 | 0.071 |

Table 3. Population growth rate ($\lambda$) of three *Zea diploperennis* populations from Sierra de Manantlán Biosphere Reserve, Mexico.

| Cycle Year | $\lambda$ | | |
|---|---|---|---|
| | Site 1 (s1) | Site 2 (s2) | Site 3 (s3) |
| 89-90 | 0.555 | 0.572 | 0.498 |
| 90-91 | 0.734 | 1.108 | 0.868 |
| 91-92 | 0.831 | 0.912 | 0.989 |
| 92-93 | 0.855 | 1.100 | 1.069 |

Using the first year from each site as a control; s1 vs. s2 ($p=0.043$), s1 vs. s3 ($p=0.031$) and s2 vs. s3 ($p=0.92$). Using first year from site 1 as a control; s1 vs. s2 ($p=0.016$), s1 vs. s3 (p=0.010) and s2 vs. s3 ($p=0.99$).

# FIGURE LEGENDS

Fig.1. The life cycle graph for *Zea diploperennis* gents $S$=seed; veg=genet without flowering shoots; 1-2 =genet with 1-2 flowering shoots; ≥3=genet with 3 or more flowering shoots.

Fig.2. (a) Total number of shoots, (b) number of reproductive shoots and (c) number of fruits of *Zea diploperennis* in each year at the three study sites (circles, site 1; squares, site 2; triangles, site 3).

Fig.3. Survivorship curves (log-scale) of ramets of *Zea diploperennis* in the three study sites, for the monthly cohorts of years 1992 and 1993.

Fig.4. Percentage of mature reproductive ears produced by monthly cohorts of ramets in the three study sites. The letters under each bar indicate the month(s) during which the cohort was established.

Fig.5. 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).
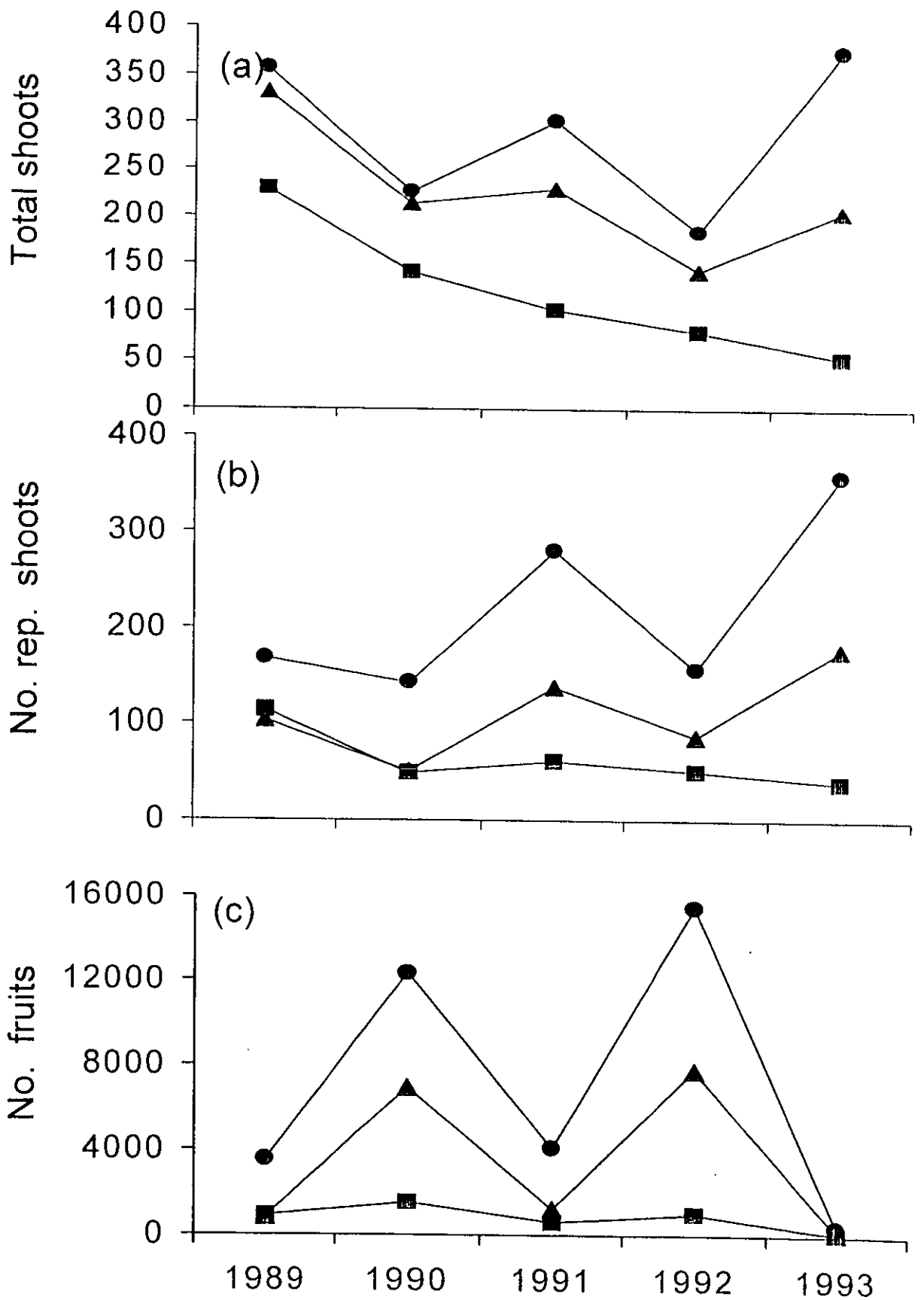
Fig.6. Relationships between population growth rate ($\lambda$) and (a) persistence, (b) sexual growth and (c) vegetative growth loops. The persistence loops and the vegetative growth loops were not significantly correlated with $\lambda$ ($r$ = 0.46 and 0.03, $p$ = 0.13 and 0.93,

respectively), but the sexual growth loops were significantly correlated with population growth ($r = 0.77$, $p = 0.004$).
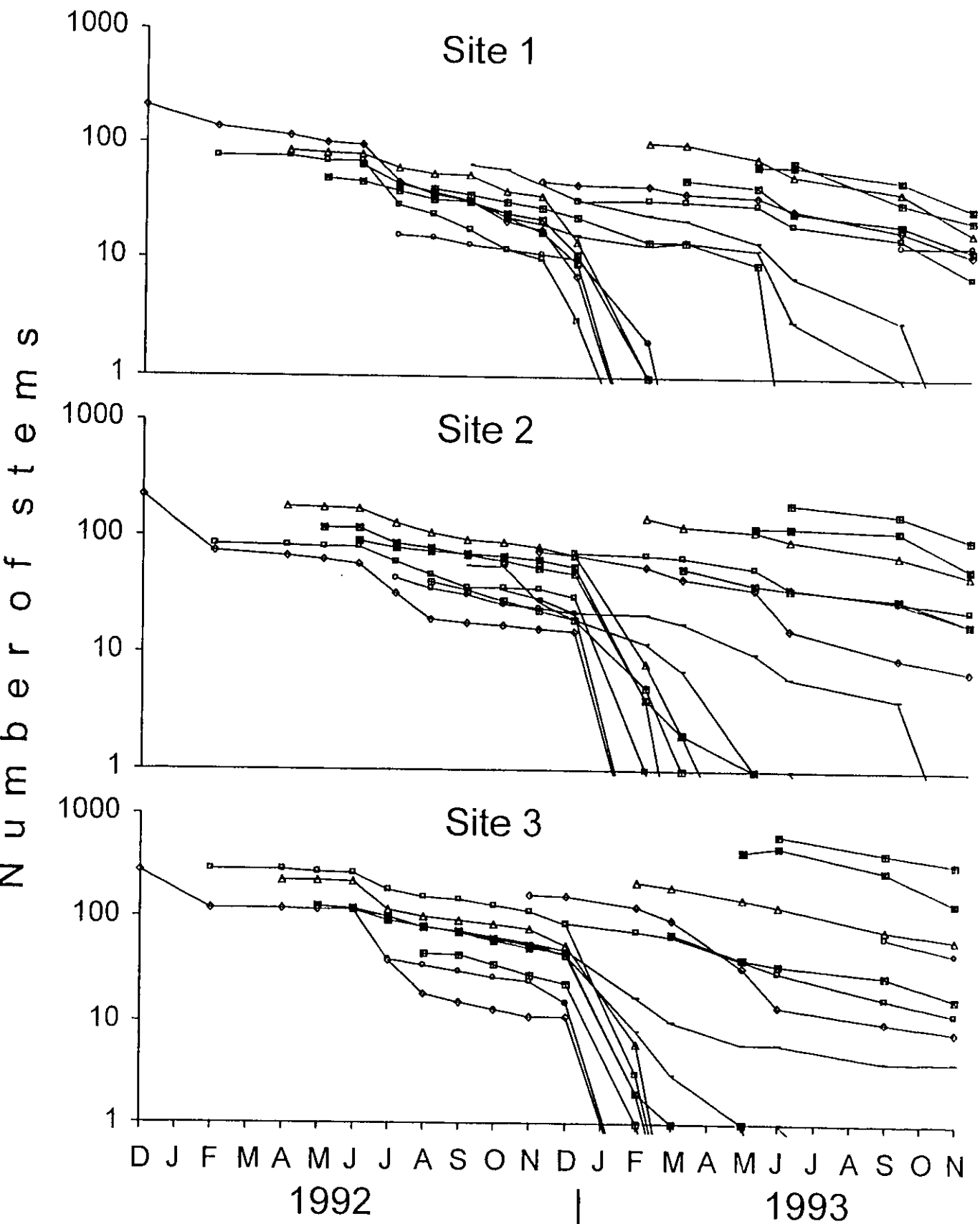
Fig.7. Simulation analysis in three *Zea diploperennis* populations, showing simulated population sizes *vs.* time. The ratio in each graph indicates frequency of simulated disturbances; for example; 1/10 indicates one simulated disturbance every ten years. The dotted lines indicate simulations projecting 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. See text for more details.
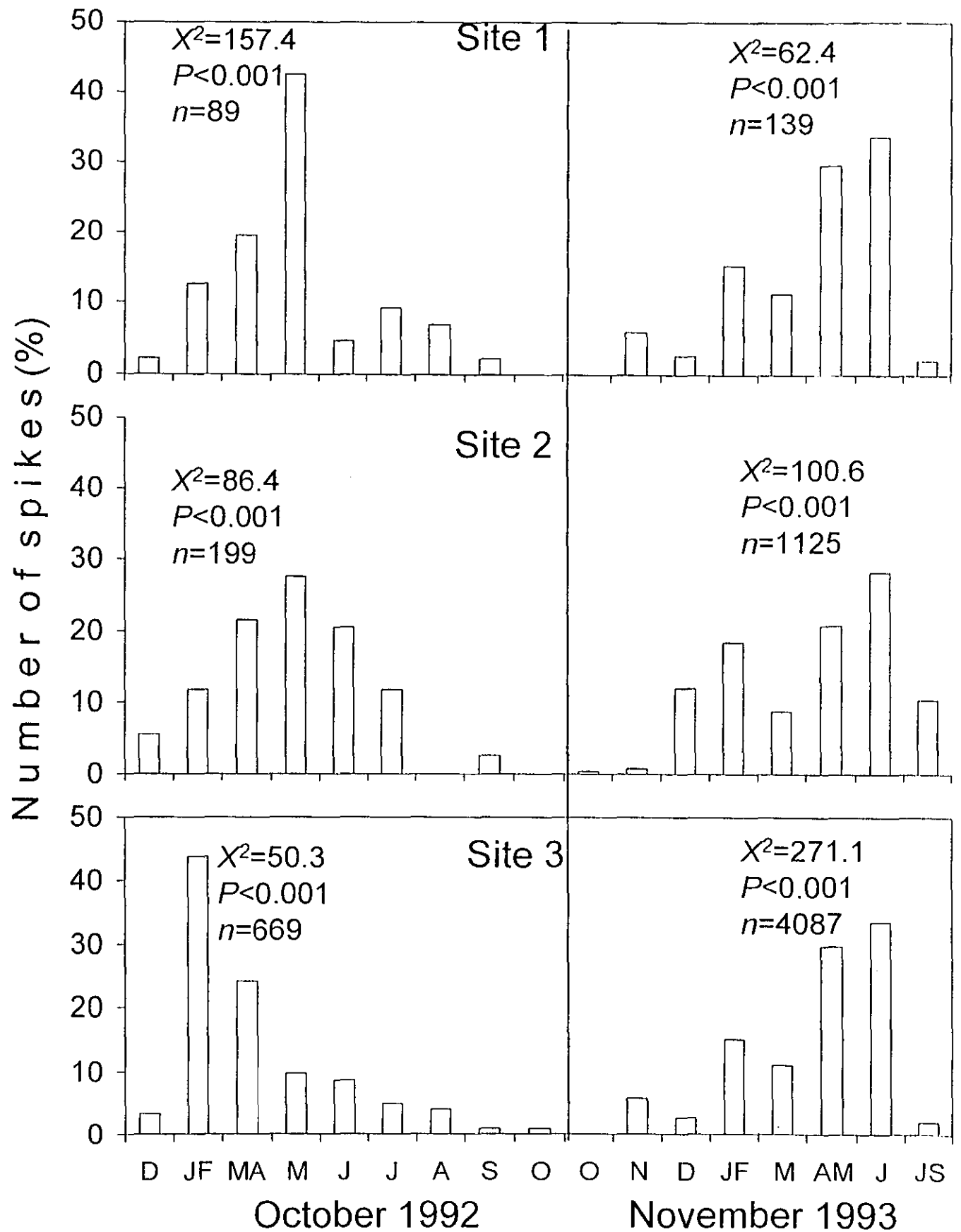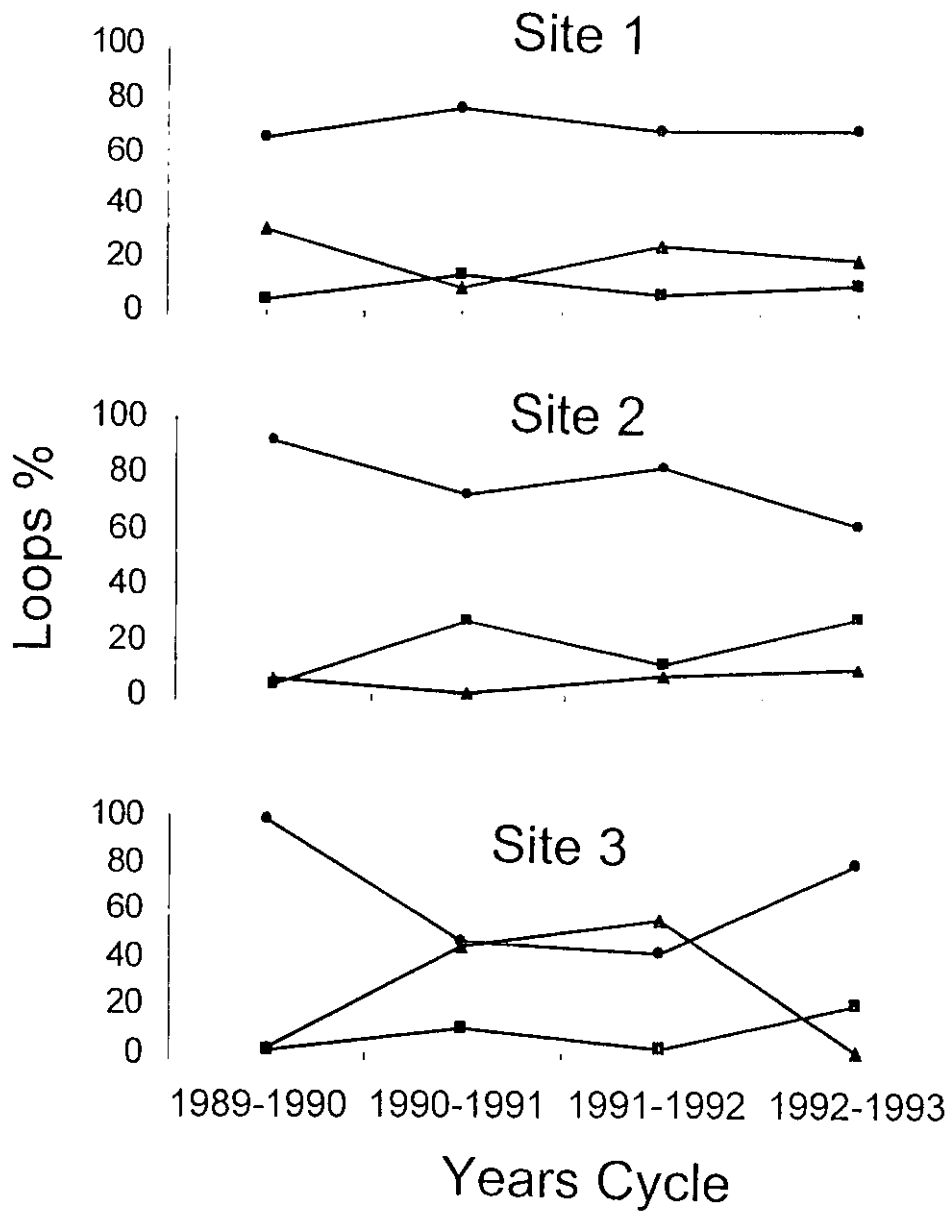
Sánchez-Velásquez et al. Fig.1
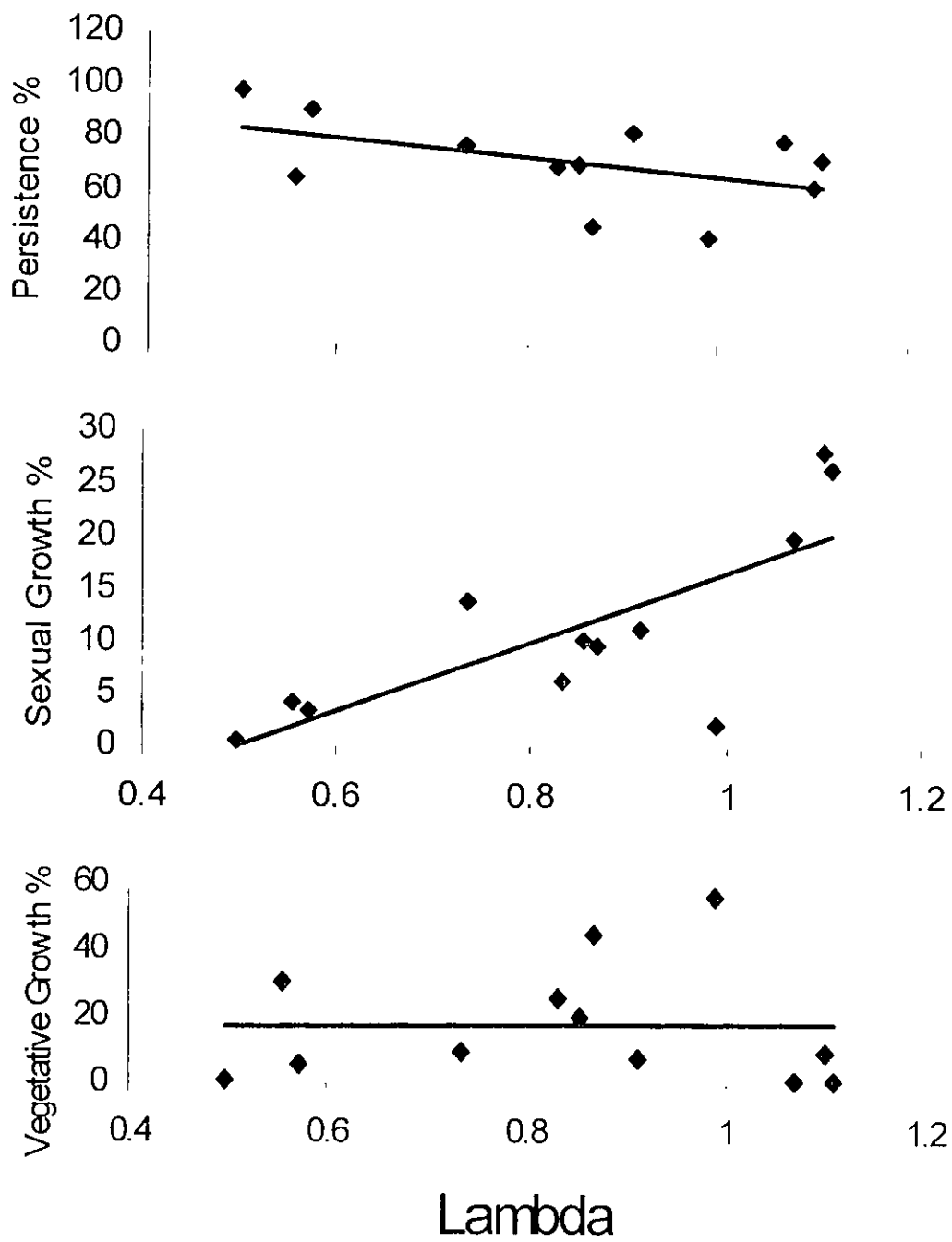
83

Sánchez-Velásquez *et al.* Fig.2

Site 1

Site 2

Site 3

D J F M A M J J A S O N D J F M A M J J A S O N

1992

1993

Sánchez-Velásquez *et al.* Fig. 3

85

X²=157.4
P<0.001
n=89

Site 1

X²=62.4
P<0.001
n=139

X²=86.4
P<0.001
n=199

Site 2

X²=100.6
P<0.001
n=1125

X²=50.3
P<0.001
n=669

Site 3

X²=271.1
P<0.001
n=4087

D JF MA M J J A S O

October 1992

O N D JF M AM J JS

November 1993
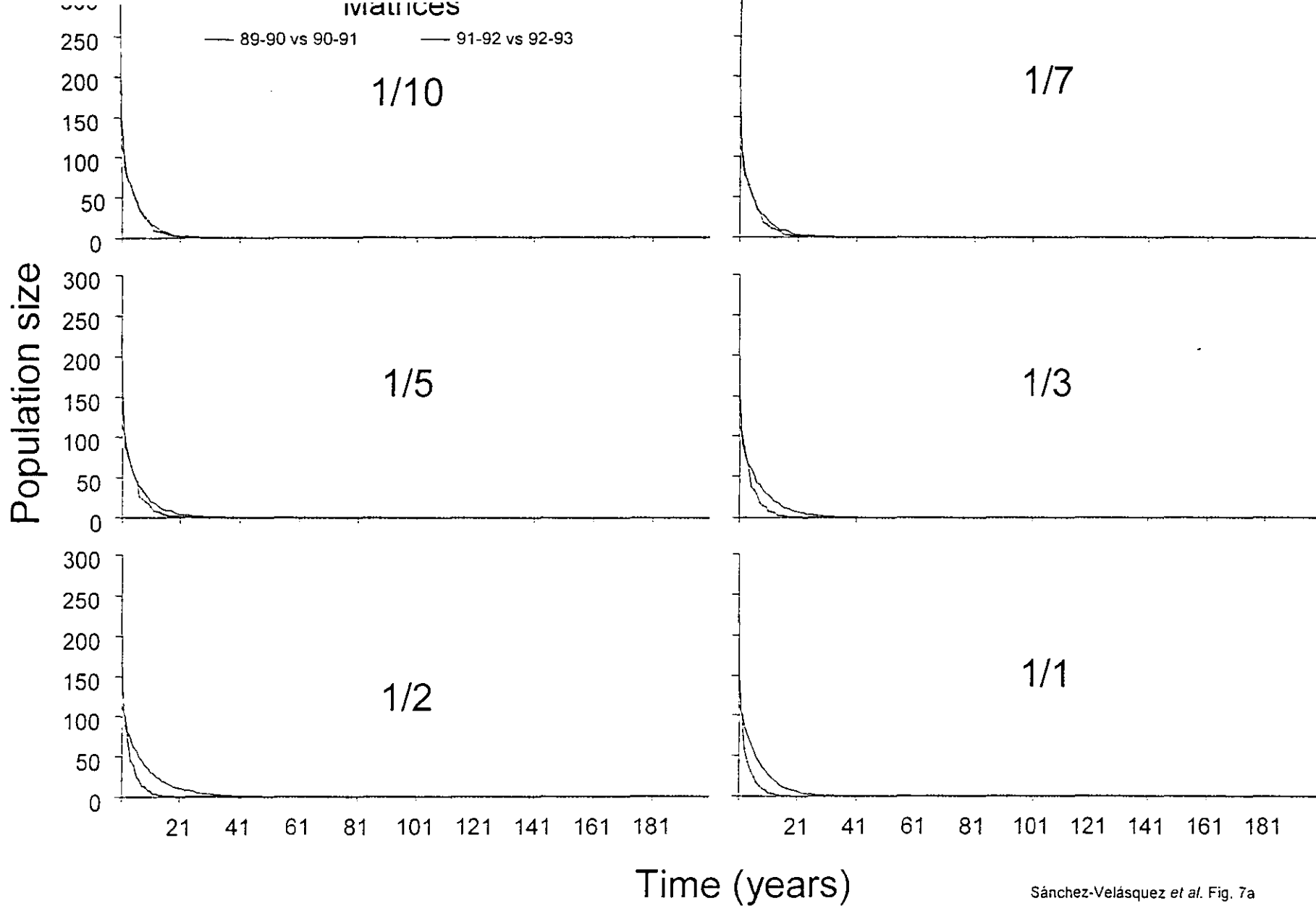
Number of spikes (%)

Sánchez-Velásquez *et al.* Fig. 5

87

Sánchez-Velásquez et al. Fig. 6

88

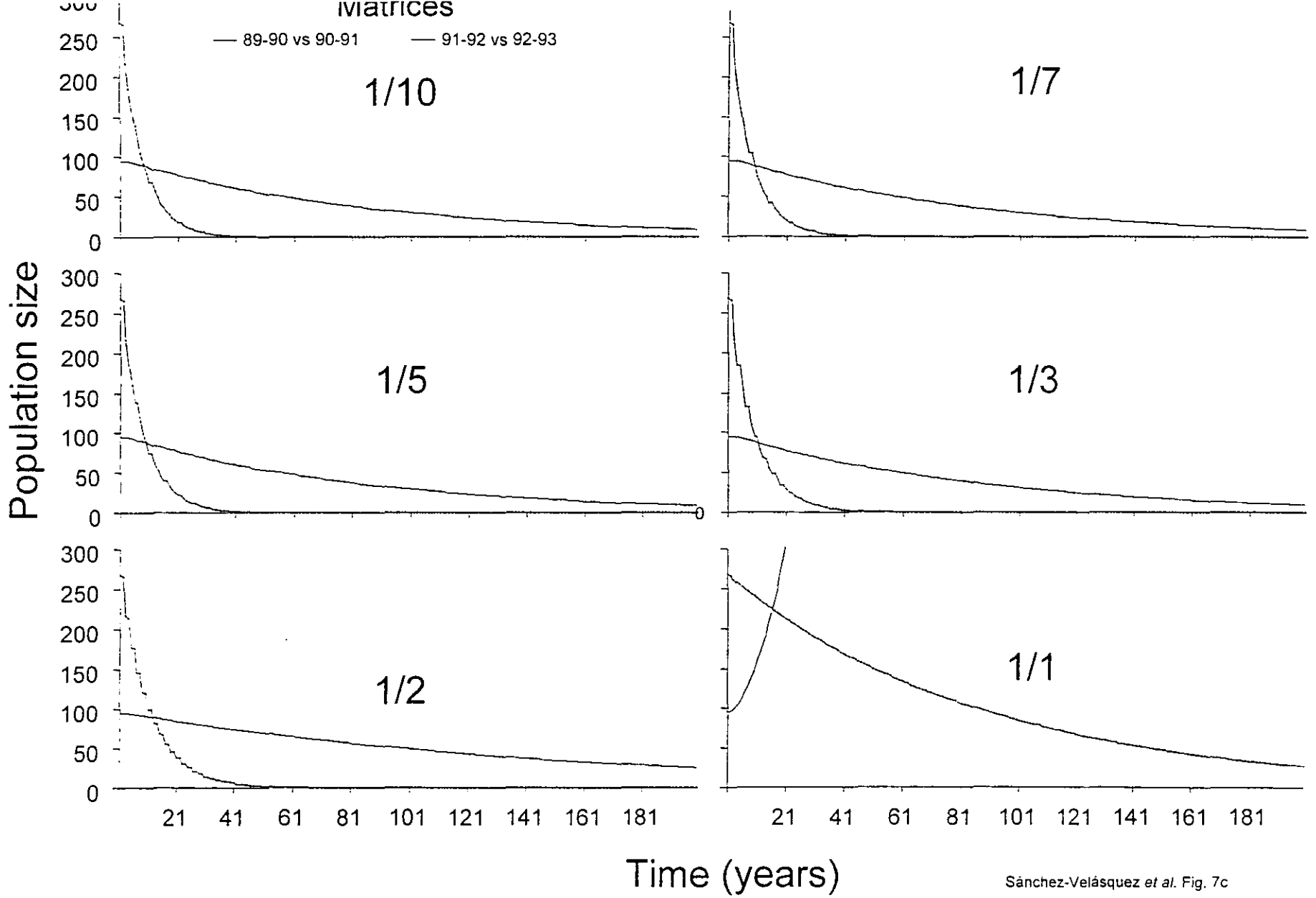Sánchez-Velásquez et al. Fig. 7a

Site 1

Sánchez-Velásquez et al. Fig. 7b

Site 2

Matrices

— 89-90 vs 90-91    — 91-92 vs 92-93

Site 3

Sánchez-Velásquez *et al.* Fig. 7c

# CAPÍTULO VI

## CONCLUSIONES Y RECOMENDACIONES

Los resultados sugieren que *Zea diploperennis* presenta un banco de frutos permanente. La mayoría de los frutos caen de los tallos y son removidos inmediatamente o germinan, solo una pequeña porción de los frutos permanecen en el suelo . Los que se mantienen adheridos a los tallos semélparos soportan la remoción y la época de sequía, que forman la principal fuente de frutos, por lo que el banco de frutos está principalmente en la parte aérea y muerta de la planta.

Los resultados nos permiten inferir que entre más corto sea el período de sequía mayor será la probabilidad de sobrevivencia de los frutos, ya que así germinarían y escaparían a la depredación por roedores. Sánchez-Velásquez y Lorente-Adame (1993) demostraron éste potencial en diferentes hábitats y profundidades del suelo, i. e., entre más enterrado esté el fruto (hasta 10 cm) mayor probabilidades de sobrevivencia tendrá y a menor cobertura vegetal, menor será la sobrevivencia.

También sugieren que *Zea diploperennis* presenta una mejor adaptación en suelos de Ultisoles que en Alfisoles, de tal manera que la tasa de incremento de individuos genéticos es mas alta en los primeros. Sin embargo no se observaron tendencias entre el estadio sucesional o factores del medio como: altitud, exposición, pendiente y tipo de suelo, *versus* los parámetros de las poblaciones de tallos.

El mayor número de tallos de cada uno de los sitios de cada año coincidió con el segundo mes de la temporada de lluvias (junio), y el número mas bajo de tallos fue observado durante el mes con menos precipitación (octubre o diciembre). La disponibilidad de agua parece favorecer el crecimiento y desarrollo de las plantas clonales (Abrahamson 1980).

La mortalidad en individuos genéticos de *Zea diploperennis*, como en otras especies de plantas rizomatosas (Harper 1977, Lovett Doust 1981), disminuye con la edad. La relación inversa entre la proporción de la mortalidad de individuos genéticos y la edad es probablemente debido a la competencia asimétrica intraespecífica (Crawley 1990), donde los individuos mas viejos establecidos son competitivamente superior a sus homólogos mas jóvenes, como ha sido demostrado para poblaciones de *Solidago canadensis* (Hartnett y Bazzaz 1985), *Fagus crenata* (Nakashizuka 1987 en Crawley 1990) y *Bouteloua gracilis* (Aguilera y Lauenroth 1993). Este patrón caracteriza a especies donde la competencia intraespecífica parece ser la responsable de la supresión de la incorporación de plántulas después de la colonización inicial (incorporación inicial del plántulas de acuerdo a Eriksson (1993)).

Como en el caso de *Ranunculus acris* y *R. bulbosus* (Sarukhán y Harper 1973), el número total de genets por sitio en poblaciones de *Z. diploperennis*, exhibió un ritmo estacional con picos durante la primavera y fue más evidente en el segundo año. La mortalidad más alta de individuos genéticos ocurrió durante la estación de mayor crecimiento, *i. e.*, la estación de lluvia (de julio a septiembre). Esto se asemeja a los patrones de mortalidad descritos para *R. canadensis* (Hartnett y Bazzaz 1985), *Lolium perenne* y otros zacates clonales (Langer *et al.* 1964, Kays y Harper 1974). Este patrón sugiere que la competencia intraespecífica puede regular la mortalidad de individuos genéticos (Sarukhán y Harper 1973).

El crecimiento mas activo del *Z. diploperennis* ocurre inmediatamente después de las primeras lluvias hasta la estación seca. Como una consecuencia, se postula que la competencia inter e intraespecífica ocurre principalmente durante la estación de lluvias, que

coincide con el periodo donde se observaron las máximas tasas de mortalidad de individuos genéticos.

La evaluación del efecto de las perturbaciones sobre los atributos de las poblaciones de *Zea diploperennis*, se demostró que esta especie responde positivamente a la roza-tumba-quema y a la roza-tumba sin quema. El efecto de la perturbación es doble, ya que afecta a las poblaciones en ambos niveles, tanto en la demografía de individuos genéticos como de tallos. A nivel de tallos, la perturbación aumentó dramáticamente el número de tallos vegetativos dentro de cada genet, y especialmente el número de tallos con mazorcas. De este modo, en el año seguido de un evento de perturbación incrementó la lluvia de frutos en el banco de frutos del suelo, seguido por una subsecuente periodo de germinación. A nivel de demografía de individuos genéticos, incrementó la germinación conduciendo un incremento en el establecimiento de plántulas, y por lo tanto en la incorporación de nuevos individuos para la población. Como lo señalan la curva tipo III de sobrevivencia de plántulas, la mayoría de las nuevas incorporaciones morirán, sin embargo, pocos eventualmente sobreviven y ayudan al mantenimiento, o incluso incrementa el número de genets.

El uso de la roza-tumba sin quema tiene efectos semejantes que aquellos causados por la roza-tumba-quema, tanto a nivel de individuo como a nivel de la población de *Zea diploperennis*. De este modo, la simple roza, tumba sin quema podría ser un factor de manejo mas conveniente para mantener las poblaciones de este teocintle. Sin alguna perturbación, la incorporación neta de nuevos individuos en las tres poblaciones de *Z. diploperennis* estudiadas durante cinco años en la zona núcleo de Manantlán-Las Joyas es casi cero. Las perturbaciones experimentales parecen ser capaces de promover el crecimiento vegetativo vigoroso y la producción masiva de frutos. El número de individuos genéticos en los tres sitios dentro de

Las Joyas está gradualmente decreciendo sin perturbaciones, y si la tendencia continua, las poblaciones pueden extinguirse localmente dentro de área núcleo de la reserva. Esto es casi irónico que la planta que dio origen al programa de conservación parece estar siendo mas pobre en el área núcleo que en la zona de amortiguamiento periférica, donde la agricultura indígena esta aún llevándose a cabo. Aunque no se ha analizado el destino de los nuevos individuos genéticos establecidos en recientes bosques talados y quemados, en este estudio, simples observaciones descriptivas sugieren que la apertura de nuevas áreas, promueve el establecimiento de nuevos individuos. Debido a los altos costos económicos y riesgos asociados a las prácticas de roza-tumba-quema en la zona núcleo de la reserva, quizá la más eficiente manera para mantener las poblaciones es a través de un sistema de un manejo metapoblacional - similar a la agricultura itinerante de roza-tumba-quema, donde las áreas de *Z. diploperennis* han sido perdidas podrían ser reabiertas y sembradas con frutos de *Z. diploperennis* -, más que tratar de preservar las poblaciones por medio de perturbaciones locales donde las poblaciones están establecidas. Estudios de diversidad genética en las poblaciones protegidas de Las Joyas comparados con las poblaciones de las áreas de amortiguamiento bajo el uso del sistema indígena tradicional puede también brindar nuevos e importantes elementos para el éxito de la conservación de *Zea diploperennis*.