Dinámica poblacional y regeneración de *Quercus rugosa*: implicaciones para la restauración de bosques de encinos

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RESUMEN

Se estudió la dinámica poblacional y la regeneración de un especie arbórea, *Quercus rugosa*, con el fin de obtener información ecológica relevante para el manejo de la población durante un programa de restauración ecológica en el Ajusco Medio, D. F.

En el primer artículo se analiza la relación entre tamaño de semillas y la supervivencia y crecimiento de plántulas de *Quercus rugosa* y *Q. laurina* en condiciones normales y bajo herbivoría simulada y/o pérdida de los cotiledones un mes después de la germinación. Los resultados muestran que: a) el tamaño de la semilla influye significativamente en la supervivencia y en la biomasa final de las plántulas de ambas especies; b) ambas especies dependen de las reservas contenidas en sus cotiledones un mes después de la germinación; c) el tamaño de la semilla influye en la capacidad de sobrevivir a la pérdida de cotiledones y a la herbivoría en *Q. rugosa*; d) la presencia de cotiledones y el tamaño de la semilla influyen en el crecimiento posterior a la pérdida de biomasa aérea por herbivoría en esta especie y, e) las plántulas de ambas especies no pueden reponerse totalmente a una pérdida de biomasa aérea por herbivoría en una temporada de crecimiento.

En el segundo artículo se analizan los factores del medio físico y biótico que influyen en la capacidad de *Q. rugosa* para establecerse y sobrevivir en los tres principales ambientes de la zona. Este trabajo mostró que: a) existe un consumo importante de bellotas por roedores, aunque una proporción variable de semillas permanece un tiempo suficiente para germinar, dadas las condiciones adecuadas; b) la germinación de semillas y el establecimiento de plántulas son más bajas en el sitio perturbado que en el borde o el interior del bosque; c) las principales causas de mortalidad de las plántulas difieren entre sitios, destacando la desecación en el sitio perturbado. En el borde del bosque se presenta la mayor supervivencia, y en caso de una temporada de secas extremosa cobran importancia los microambientes que ocupan las plántulas, ya que se registra una mayor supervivencia en micrositios parcialmente sombreados en comparación con la de micrositios abiertos o totalmente sombreados; d) en el borde de bosque se presenta una correlación positiva entre tamaño de la semilla y supervivencia de las plántulas y, e) el crecimiento de las plántulas es menor en el interior del bosque.

El tercer trabajo, que aborda el estudio de la dinámica poblacional de Q. *rugosa* en el borde del bosque mostró que, en las condiciones actuales, la población se encuentra estable, con una tasa de crecimiento poblacional de 1.003. Las limitaciones que presenta el crecimiento poblacional pueden deberse tanto a las características de la especie como a las condiciones poco favorables del malpaís. Se exploró mediante simulaciones el impacto que tendría la aplicación de distintas técnicas diseñadas para favorecer el crecimiento poblacional. La realización de aclareos, o eliminación de ramas de árboles y arbustos para favorecer el crecimiento de individuos supresos de las categorías de brinzales (saplings) y juveniles, tiene un impacto limitado cuando se dirige a una sola categoría de tamaño, mientras que si se aplica simultáneamente a la mitad de los individuos supresos de las tres categorías consideradas, produce un crecimiento cercano al 2% anual. La introducción artificial de plántulas también permite incrementar la tasa de crecimiento poblacional: si se duplica el ingreso anual respecto de los valores encontrados en condiciones naturales se obtendría un valor de 1% anual, mientras que si se triplica la entrada de plántulas se obtiene 2%. Finalmente, en la búsqueda de lograr un mayor incremento en el crecimiento poblacional, se encontró que ambas técnicas se pueden combinar, y bajo este escenario se obtienen los mejores resultados, pues el crecimiento poblacional supera el 4% anual.

En resumen, la reinvasión de encinos al matorral perturbado sólo se produciría, en condiciones naturales, en tiempos sucesionales muy grandes, dada la tasa de crecimiento poblacional encontrada. Por ello, si se desea reintroducir esta especie al matorral perturbado es necesario realizar prácticas de manejo cuidadosas encaminadas a favorecer la regeneración, i. e. el establecimiento y el crecimiento de las plántulas. No resulta recomendable la siembra de semillas, y sí la introducción artificial de plántulas, poniendo especial cuidado en la selección de sitios semisombreados que simulen el ambiente del borde del bosque. En el caso de utilizarse plántulas jóvenes producidas en vivero, es aconsejable hacer una selección previa de las semillas grandes. La introducción artificial de plántulas, conjuntamente con la eliminación del sombreado que limita el crecimiento de los brinzales y juveniles ya establecidos, produciría los mejores resultados. Sin embargo, incluso con la realización de estas prácticas, la recuperación de la población de *Quercus rugosa* en el malpaís no se llevará a cabo en el corto plazo.

ABSTRACT

The population dynamics and regeneration of an oak population (*Quercus rugosa*) was studied in order to obtain relevant ecological information regarding the management of the population during an ecological restoration program in the Ajusco Medio, D. F.

The first paper analyses the relationship between seed size and seedling survival and growth of seedlings of *Quercus rugosa* and *Q. laurina* on normal conditions and under simulated herbivory and/or cotyledon loss, one month after germination. The results show that: a) seed size has an effects on seedling survival and final biomass of both species, b) both species depend on their cotyledon reserves one month after germination, c) seed size has an influence on the ability to survive cotyledon loss and herbivory on *Q. rugosa*, d) cotyledons and seed size influence growth after an event of herbivory in this species, and e) seedlings of both species are unable to fully recover from aerial biomass loss by herbivory in one growing season.

The second paper analyses the physical and biological factors that influence the establishment and survival of *Q. rugosa* in the three environments of the study site. The results show that: a) there is an important seed consumption by rodents, although variable proportions of seed remain on the ground long enough to germinate, given the right conditions, b) seed germination and seedling establishment are lower on the disturbed site than in the forest border or the forest interior, c) the main causes of death vary between sites, with desiccation being particularly important at the disturbed site, d) there is a positive correlation between seed size and seedling survival at the forest border and, e) seedling growth is lower at the forest interior.

The third paper, dealing with the population dynamics of *Q. rugosa* at the forest border, showed that under present conditions, the population is stable, with a population growth rate of 1.003. The limited population growth may be explained both by the specie's characteristics and by the harsh conditions of the malpaís. By means of simulations, the impact of diverse techniques devised to increase population growth was assessed. The

removal of tree branches and shrubs that keep saplings and juveniles suppressed has a limited impact if focused in only one size category, while it produces around 2% if it is applied to half the suppressed individuals of the sapling and juveniles category. The artificial introduction of seedlings was also simulated: if recruitment duplicates with respect to the values found under natural conditions, a 1% annual population growth would be obtained, while if seedling input is triplicated a 2% is obtained. Finally, in order to attain a higher increment in population growth, both techniques can be used simultaneously, and it is under these conditions that the best results are obtained, with an annual population growth over 4%.

To resume, the re-invasion of oaks to the disturbed shrubland growing on the basaltic rock only would happen along a large successional time, given the population growth rate. If this species is to be re-introduced to the disturbed shrubland, it is necessary to carry careful management practices aimed at favouring regeneration, i. e. the establishment and growth of seedlings. It is not advisable to use seeds, but it is to artificially introduce seedlings, taking special care to select semi-shaded microsites that simulate the environment of the forest border. In case of using young seedlings raised in a nursery, it is convenient to select large seed sizes. The artificial re-introduction of seedlings, along with the clearing of the shade that limits growth of established sapling and juveniles, would render the best results. However, even with these management practices, the recovery of the *Quercus rugosa* population in the shrubland will not be achieved in the short term.

CAPÍTULO I

INTRODUCCIÓN

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Introducción

El género *Quercus* reviste gran importancia, tanto por su diversidad como porque incluye numerosas especies de árboles dominantes de los bosques templados del hemisferio norte. Se calcula que existen alrededor de 450 especies de *Quercus* (González Rivera 1993), de las cuales poco más de un tercio se encuentra en México, lo que coloca a nuestro país como el de mayor diversidad de encinos en el continente americano. La sistemática de los taxa pertenecientes a este género se encuentra todavía lejos de ser satisfactoria, pero diversos autores coinciden en que nuestro país posee entre 150 y 200 especies de *Quercus* (Rzedowski 1981, González Rivera 1993, Nixon 1993).

En el continente americano se encuentran encinos desde el sur de Canadá hasta el norte de Colombia. En México los encinares, junto con los pinares, constituyen la mayor parte de la cubierta vegetal de las zonas montañosas. Predominan en áreas de clima templado, aunque se pueden encontrar en otras condiciones climáticas, desde tropicales hasta semiáridas, por lo que existen encinos en todos los estados de la República excepto Yucatán y Quintana Roo (Rzedowski 1981). A esta diversidad de condiciones ecológicas se asocia un intervalo muy amplio de formas de crecimiento, desde arbustos rizomatosos de baja estatura en pendientes secas y montañas altas, hasta grandes árboles con contrafuertes en bosques húmedos de tierras bajas (Nixon 1993).

A pesar de la gran diversidad florística, fisonómica y ecológica de los encinares mexicanos, existen aún grandes carencias en el conocimiento biológico de los mismos. Si bien en fechas recientes se han hecho revisiones taxonómicas para varios estados de la República Mexicana, la filogenia del grupo permanece incierta y numerosas especies descritas deben ser revisadas, por lo que aún no existe un estudio completo de las especies de *Quercus* en México (Nixon 1993). En relación a la ecología de los encinares, la mayoría de los trabajos publicados se reduce a descripciones de los ambientes en los que se encuentran las distintas especies a nivel local o regional, y aunque existen algunos trabajos que abordan diversos aspectos de la regeneración y el manejo de unas cuantas especies (Quintana Ascencio 1989, Eckelman 1995, Moreno et al. 1995, Garza Caligaris 1997, Zavala y García Moya 1997, Cabrera et al. 1998, López Barrera 1998), puede afirmarse que no existe información ecológica básica de la mayor parte de las especies mexicanas de encinos. Este conocimiento resulta indispensable si se pretende frenar el deterioro ecológico en las zonas montañosas templadas del país o, como en el presente caso, si se emprende la restauración ecológica de zonas antes ocupadas por encinares.

Debido a que los bosques de encino generalmente se localizan en regiones climáticas favorables para la población humana, y a que originalmente ocupaban áreas particularmente aptas para el desarrollo de la agricultura, han sido de los tipos de vegetación más afectados por el impacto del hombre (Rzedowski 1981). Esto ha tenido como resultado su eliminación casi total de los terrenos bajos y poco accidentados, mientras que en los terrenos escarpados sufren un fuerte deterioro causado por la introducción de ganado o por estar sujetos a explotación forestal. En el primer caso, el pastoreo intenso y la aplicación frecuente de fuego ocasionan problemas que van desde

la ausencia de regeneración y la degradación del sotobosque, hasta problemas serios de erosión. En el caso de la explotación forestal, el impacto varía dependiendo del terreno y de la intensidad de la misma, pero en casos severos puede llevar a la desaparición extensiva de zonas boscosas. De acuerdo con Rzedowski (1981), grandes extensiones de encinares se consumieron en el siglo pasado debido a su explotación desmedida para la obtención de carbón vegetal, que fue el principal combustible de uso doméstico durante muchos años en amplias regiones del país. En la actualidad, a la explotación comercial de encinares, (calculada en 440×10^3 m^3 por la SARH, Masera et al. 1997), debe añadirse la realizada para el consumo local de los asentamientos rurales. El impacto de esta última debe ser considerable, ya que la leña de encino es el combustible doméstico preferido por la población campesina de las zonas templadas del país.

Los encinares son el hábitat de una gran variedad de animales y con gran frecuencia ocupan sitios estratégicos en muchas cuencas hidrológicas, por lo que su deterioro tiene efectos dañinos, no sólo en la zona donde se produce el disturbio, sino a un nivel regional. Además de la pérdida de biodiversidad que conlleva su eliminación, ésta puede ocasionar erosión, desecación de manantiales, contaminación del agua, inundaciones y azolve de presas, entre otros efectos (Gómez Pompa 1985).

Lo anterior implica que tanto la conservación de estas comunidades, como la restauración de al menos una parte de la zonas antes ocupadas por encinares resulta una tarea urgente. Es en este contexto que se plantea el presente trabajo, el cual pretende brindar información ecológica básica que dé sustento a la restauración de un bosque de encinos (*Quercus rugosa*) en el Ajusco Medio, D. F.

Los valles intermontanos en que se asentaban muchos bosques de encino y de pino-encino has estado ocupados desde tiempos remotos, y en la actualidad sobreviven sólo relictos de estos tipos de vegetación en las regiones densamente pobladas, como el Valle de Toluca, el Valle de Puebla y Tlaxcala, el Valle de Chihuahua, la Mesa de Michoacán, los valles de Jalisco, la Llanura de Comitán, y desde luego, el Valle de México (Challenger 1998). Aunque no se dispone de datos recientes, se sabe que tan sólo en la Sierra del Ajusco, al el sur de la ciudad de México, el avance de la mancha urbana destruyó entre los años de 1959 y 1977 un total de 992 ha de bosque de encino, 945 ha de bosque de pino-encino y 800 de pedregal (parte del cual estuvo poblado por encinos, Benitez et al. 1987). Por otra parte, Aragón (1993) calcula que en el periodo de 1950 a 1991 se perdieron 1314 ha en el Ajusco Medio, zona en que se realizó el presente trabajo, y concluye que hacia fines de los años setentas los asentamientos urbanos irregulares que se establecieron en esta zona tuvieron un impacto ecológico irreversible, sobre todo en el encinar representado por *Quercus rugosa*.

Debido a la importancia que tiene el Ajusco Medio para la recarga de los acuíferos que abastecen a la ciudad de México y por ser una zona que aún alberga una alta biodiversidad, a partir de 1990 se inició un proyecto de restauración ecológica en la zona sujeta a conservación ecológica denominada Parque Ecológico de la Ciudad de México (Bonfil et al. 1997). Para lograr el restablecimiento de la vegetación en las áreas perturbadas se consideró necesario estudiar con detenimiento a ciertas especies importantes para el funcionamiento del ecosistema. Debido a que los encinos son elementos dominantes del paisaje, se abordó el estudio de las condiciones que permiten la regeneración de la especie más abundante (*Quercus rugosa*), así como el estudio de su dinámica poblacional.

El realizar estudios ecológicos detallados en ambientes perturbados por el hombre presenta una relevancia doble. En primera instancia, constituyen el puente entre la teoría ecológica y la solución práctica de problemas de restauración, conservación y explotación de comunidades biológicas. En este sentido la tarea consiste en aplicar los conceptos ecológicos básicos en condiciones particulares, con el objeto de elaborar herramientas de conservación y restauración ecológica. En segundo término, las comunidades alteradas pueden ser sistemas clave para documentar fenómenos ecológicos que no son aparentes en ambientes naturales, además de aumentar el cúmulo de conocimientos ecológicos básicos de las especies involucradas. De esta forma, la restauración ecológica permite plantear interrogantes básicas y poner a prueba ideas fundamentales que forman la base de la teoría ecológica (Jordan et al. 1987).

Debido a que la restauración activa consiste en gran medida en un proceso de producir cambios que ocurrirían de manera natural dado un tiempo suficiente, pero en un tiempo mucho menor, la restauración puede ser considerada como un intento de imitar la sucesión para poder controlarla (Ashby 1987, Luken 1990). En el caso particular de la especie que nos ocupa, el establecimiento de los encinares en la zona del Ajusco Medio ha sido el resultado de un proceso sucesional, en el cual esta especie invadió, a lo largo de varios cientos de años, el área ocupada por el pedregal o malpaís, de la cual fue eliminada por la perturbación que significó el establecimiento de asentamientos urbanos irregulares. Esto llevó a la consideración de que el estudio del comportamiento poblacional de *Quercus rugosa* en los distintos ambientes de la zona permitiría, además de hacer una contribución importante para la restauración ecológica, probar ideas acerca de como esta especie, y la comunidad dominada por ella, se desarrolla y funciona.

Es en este contexto que se plantearon las investigaciones incluidas en la presente tesis. El análisis ecológico realizado se abordó principalmente en el nivel de las poblaciones. El uso de la herramienta demográfica se consideró esencial, ya que mediante el análisis de los cambios numéricos en distintos estadios del ciclo de vida es posible comprender las causas de los cambios espaciales y temporales en el tamaño de las poblaciones (van Groenendael et al. 1988, Caswell 1989) y, en este caso, de los cambios del elemento fisonómico más importante de la comunidad. La identificación de los principales factores, tanto extrínsecos como intrínsecos que regulan el crecimiento poblacional, permitirá evaluar la pertinencia de diversas técnicas encaminadas a favorecer la recuperación de las poblaciones en aquellos lugares de los cuales fue eliminada a causa de perturbaciones antropogénicas.

Paralelamente al estudio de la dinámica poblacional, se consideró importante analizar con mayor detalle los fenómenos implicados en la regeneración de esta especie. Estudios previos han reportado problemas con la regeneración de varias especies de *Quercus* en zonas muy diversas (Carvell y Tryon 1961, Shaw 1968, Griffin 1971, Crow 1988, 1992), lo que ha permitido suponer que esta especie, al igual que otras del género, puede requerir de condiciones muy específicas para su regeneración exitosa. Por ello, se decidió abordar el estudio del nicho de regeneración de *Quercus rugosa* (sensu Grubb 1977), con el fin de aportar información detallada que permitiera entender mejor la dinámica de las fases tempranas de desarrollo de esta especie en condiciones naturales, así como brindar bases sólidas para la elaboración de planes de recuperación.

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Finalmente, se abordó un tercer nivel de estudio, que aborda un problema particular que puede tener consecuencias a nivel poblacional. En éste se analizaron experimentalmente, en condiciones controladas, dos factores que se pensaba podrían incidir en el establecimiento temprano de las plántulas: el tamaño de la semilla y la herbivoría. Con este trabajo se buscó tanto obtener información ecológica básica como contribuir al debate actual sobre el efecto que tiene la variación en la cantidad de reservas almacenadas en las semillas en el desempeño de las plántulas, tanto en condiciones óptimas como cuando están sujetas a algún tipo de estrés, en este caso el causado por la pérdida de biomasa aérea como resultado de la herbivoría. En un intento por alcanzar un mayor nivel de generalización y a la vez tener un punto de comparación, en esta investigación se incluyó a otra especie de encino, *Quercus laurina* (Humb. & Bondp.), que es común en la zona de estudio.

Con la finalidad de hacer más lógica y fluida la presentación, el orden en que aparecen los trabajos es el inverso al que se esbozó anteriormente, de tal forma que esta tesis inicia con el estudio más detallado del desempeño de plántulas en condiciones controladas y finaliza con el análisis de la dinámica poblacional. Con esto se pretende, en la medida de lo posible, integrar los resultados más relevantes obtenidos en los estudios realizados a un nivel más fino al abordar un nivel de análisis más general. De acuerdo con lo anterior, en el capítulo II de esta tesis se presenta el artículo "The effects of seed size, cotyledon reserves and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae)". En él se evalúan los efectos que tienen la variación en el tamaño de la semilla y la presencia o ausencia de cotiledones en la supervivencia y el crecimiento de plántulas de *Quercus rugosa* y *Quercus laurina* un mes después de iniciada la germinación, tanto en condiciones normales como en presencia

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de herbivoría (simulada). Mediante un experimento de invernadero se buscó responder a las siguientes preguntas: 1) ¿ está la capacidad de las plántulas de un mes de edad de sobrevivir a la pérdida de los cotiledones relacionada con el tamaño de la semilla?, 2) ¿contribuyen a la supervivencia y el crecimiento posterior de las plántulas las reservas que en ese momento permanecen aún en los cotiledones?, 3) ¿la herbivoría y el tamaño de la semilla interactúan en su efecto sobre la supervivencia y el crecimiento de las plántulas?, y 4) ¿qué consecuencias tiene la remoción de los cotiledones en la respuesta de las plántulas a la herbivoría?.

En el tercer capítulo se presenta el trabajo titulado "Seedling dynamics of *Quercus rugosa* as a tool for its reintroduction in a disturbed landscape", el cual busca establecer cuáles son los factores que inciden de manera importante en el establecimiento de las plántulas y su posterior supervivencia y crecimiento en condiciones naturales, con la finalidad de definir lo que constituye un "sitio seguro" (sensu Harper 1977) para esta especie. Para ello se adoptó un enfoque experimental, evaluando la remoción de bellotas, la germinación, el establecimiento de plántulas y su crecimiento y supervivencia a lo largo de dos años en tres condiciones contrastantes: el interior del bosque, el borde del bosque -que constituye una zona de transición entre el bosque y el matorral-, y el matorral perturbado. Del análisis de los factores del medio físico y biótico que afectaron el desempeño general de las plántulas, así como de aquéllos que resultaron particularmente relevantes en cada condición, se pretende extraer herramientas que coadyuven al manejo de las plantaciones en la zona del Ajusco Medio y otras similares en las serranías que rodean a la cuenca de México.

En el último trabajo (que se presenta en el penúltimo capítulo), titulado "A demographic analysis of an oak population (*Quercus rugosa*) in central Mexico: implications for restoration", se aborda el análisis de la dinámica poblacional de esta especie, mediante el uso de matrices de proyección poblacional de tipo Lefkovitch (1965). Esta herramienta de análisis se consideró adecuada, tanto por la relevancia que tiene el tamaño en el desempeño de los individuos para muchas especies vegetales, como por la imposibilidad de asignar una edad a los individuos de esta especie, debido a la ausencia de anillos de crecimiento en su leño (De la Paz O. comunicación personal). En este estudio se planteó evaluar el estado de la población bajo las condiciones actuales proyectadas hacia el futuro (i. e., si se encontraría estable, creciendo o decreciendo), así como identificar aquellos estadios críticos para la dinámica poblacional. Adicionalmente se analizó, por medio de la modificación de algunas entradas de la matriz, el impacto que tendrían diferentes prácticas de manejo diseñadas con el fin de favorecer el crecimiento poblacional. En virtud de estos resultados se discuten posibles prácticas de manejo dentro del programa de restauración de la especie en la zona.

Bibliografía

Ashby W. C. 1987. Forests. En: Jordan III W.R., M. E. Gilpin y J. D. Aber (eds). Restoration Ecology. A synthetic approach to ecological research. Cambridge Univ. Press

Benítez G., A. Chacalo e I. Barois. 1987. Evaluación comparativa de la pérdida de cubierta vegetal y cambios en el uso del suelo del sur de la Ciudad de México. En: E. H. Rapoport e I. López Moreno (eds). Aportes a la ecología urbana de la Ciudad de México. Instituto de Ecología y Museo de Historia Natural de la Ciudad de México. MAB-Limusa-Noriega eds. México

Bonfil C., I. Pisanty, A. Mendoza and J. Soberón. 1997. Investigación y restauración ecológica: el caso del Ajusco Medio. Ciencia y Desarrollo 135:15-23.

Cabrera L., P. Mendoza, V. Peña, C. Bonfil y J. Soberón. 1998. Evaluación de una plantación de encinos (Quercus rugosa Neé) en el Ajusco Medio, Distrito Federal. Agrociencia 32: 149-156

Carvell K. L. y E. H. Tryon. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. Forest Science 7: 98-105.

Caswell H. 1989. Matrix population models. Sinauer, Sunderland, Massacusetts.

Challenger A. 1998. Utilización y Conservación de los Ecosistemas Terrestres de México. Pasado, Presente y Futuro. CONABIO. Instituto de Ecología UNAM y Agrupación Sierra Madre S.C. México.

Crow T. R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)- A review. Forest Science **34**:19-40

Crow T.R. 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. Oecologia **91**:192-200

Eckelmann C. M. 1995. Regeneración y dinámica natural de un bosque de pino-encino en la Sierra Madre Oriental, en el noreste de México. En: *III Seminario Nacional sobre utilización de encinos*. Reporte Científico Número Especial 15. Facultad de Ciencias Forestales, Universidad Autónoma de Nuevo León. pp: 199-212

Garza Caligaris L. E. 1997. Las ectomicorrizas como elementos para evaluar y restaurar bosques de encino: un caso de estudio en la reserva ecológica del Ajusco. Tesis Maestría en Ciencias (Biología Vegetal). Facultad de Ciencias, UNAM.

Goméz Poma A. 1985. Los recursos bióticos de México (Reflexiones). INIREB y Alhambra Mexicana. México.

González Rivera R. 1993. La diversidad de los encinos mexicanos. Rev. Soc. Mex. Hist. Nat. **XLIV**: 125-142

Griffin J. R. 1971. Oak regeneration in the upper Carmel Valley, California. Ecology **52**: 862-868

Grubb P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. **52**:107-145.

Harper J. 1977. *Population Biology of Plants*. Academic Press, New York.

Jordan III W.R.. M. E. Gilpin y J. D. Aber (eds). 1987. Restoration Ecology. A synthetic approach to ecological research. Cambridge Univ. Press.

Lefkovitch L. P. 1965. The study of population growth in organisms grouped by stages. Biometrica **21**: 1-18

López Barrera F. 1998. Germinación y establecimiento temprano de *Quercus rugosa* y sus implicaciones en la rehabilitación de habitats pinarizados en Los Altos de Chiapas, México. Tesis Biología. Facultad de Ciencias. UNAM.

Luken J. O. 1990. Directing ecological succession. Chapman and Hall, Londres.

Masera O. R., M. J. Ordoñez y R. Dirzo. 1997. Carbon emissions from Mexican forests: current situation and long-term scenarios. In: *Climatic Change* (pp. 265-295)

Moreno Gómez S., M. Olvera Vargas y B. L. Figueroa Rangel. 1995. Sistemas silvícolas para encinares en Cerro Grande, Sierra de Manantlán. Jalisco. En: *III Seminario*

Nacional sobre utilización de encinos. Reporte Científico Número Especial 15. Facultad de Ciencias Forestales, Univ. Autónoma de Nuevo León. pp: 301-319

Nixon K. C. 1993. The genus Quercus in México. En: Ramamoorthy T. P. , Bye R. and J. E. Fa (eds). *Biological Diversity of Mexico*. Oxford University Press.

Quintana Ascencio P. 1989. La condición sucesional de dos encinos dominantes (*Quercus laurina* Humb. & Bonpl. y *Quercus crispipilis* Trel.) de los bosques templados de los Altos de Chiapas. Tesis Maestría en Ciencias. Colegio de Postgraduados de Chapingo. México.

Rzedowski J. 1981. *Vegetación de México*. Ed. Limusa, México.

Shaw M. W. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petrea*) in North Wales. I. A preliminary study of acorn production, viability and loses. Journal of Ecology **56**:565-583.

Zavala Chávez F. y E. García Moya. 1997. Plántulas y rebrotes en la regeneración de encinos en la Sierra de Pachuca, Hidalgo. Agrociencia **31**: 323-330

van Groenendael J. M., H. de Kroon y H. Caswell. 1988. Projection matrices in population biology. Trends in Ecology and Evolution **3**: 264-269

CAPÍTULO II

Efectos del tamaño de la semilla,

las reservas cotiledonarias y la

herbivoría en la supervivencia y

crecimiento de plántulas de

Quercus rugosa

y *Q. laurina* (Fagaceae)

Nicolas Moreno
1986

THE EFFECTS OF SEED SIZE, COTYLEDON RESERVES, AND HERBIVORY ON SEEDLING SURVIVAL AND GROWTH IN *QUERCUS RUGOSA* AND *Q. LAURINA* (FAGACEAE)[1]

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In a greenhouse experiment, seedling survival of two oak species (*Quercus rugosa* and *Q. laurina*) was greatly affected by the excision of cotyledons 1 mo after germination, with a greater impact on *Q. laurina*. The effect of seed size was also significant for both species, with a positive correlation between seed mass and survival and growth. The effect of cotyledon excision on seedling growth persisted throughout the first growing season in *Q. rugosa* and was not analyzed for *Q. laurina* due to the low number of seedlings that survived cotyledon excision. Seed size significantly affected seedling height, diameter, leaf area, and biomass at 6 mo. Seed size and cotyledon retention affected the ability of *Q. rugosa* to recover from herbivory, as both factors had a significant effect on relative growth rates after aerial biomass removal. The results show that seedlings originating from large seeds can better endure loss of cotyledons and aerial biomass and thus are better equipped to confront stress early in their lives.

Key words: aerial biomass removal; Fagaceae; *Quercus*; seed reserves; seedling survival and growth.

The role of seed size in seedling performance has received considerable attention (Foster, 1986; Mazer, 1989; Seiwa and Kikuzawa, 1991; Westoby, Jurado, and Leishman, 1992). The wide differences in seed size among species have been related to the ecological conditions in which plants establish, with species from open habitats having lower average seed mass than species from more closed habitats (Salisbury, 1942, 1974; Foster and Janson, 1985; Mazer, 1989; but see Kelly and Purvis, 1993). Large-seeded species also have an advantage in competitive environments (Gross, 1984) and when seedlings experience defoliation (Armstrong and Westoby, 1993), shade (Leishman and Westoby, 1994), or moisture stress (Baker, 1972).

Some of the patterns detected in comparisons among species are also found within species. In four of five species studied, Werner and Platt (1976) showed that populations in an open community had smaller seeds than those in a more closed community. Wulff (1986) showed that seedlings of *Desmodium paniculatum* from large seeds were favored in the early stages of growth in a dry, disturbed site. McWilliams, Landers, and Mahlstede (1968) suggested that large seed size was advantageous for *Amaranthus retroflexus* in the short growing seasons characteristic of high latitudes, although Schimpf (1977) argued that moisture availability was more important than length of the growing season, due to the increased capacity of seedlings from large seeds to establish roots in deeper soil horizons. Safe-site requirements of small seeds are more restrictive than those for larger seeds in

Prunella vulgaris (Winn, 1985) and a positive relationship among seed size and seedling establishment and growth has been reported in a variety of species (Weis, 1982; Stanton, 1984; Weller, 1985), including oaks (McComb, 1934; Tecklin and McCreary, 1991). Intraspecific studies of wild species are critical for gaining an understanding of the ecological significance of seed mass, but in oaks there have been few attempts to explore the relationship between seed size and the performance of seedlings under a variety of ecological conditions (Tripathi and Kahn, 1990).

Oaks are frequently dispersed by jays and small rodents, which are also their main seed predators (Mellanby, 1968; Shaw, 1968; Darley-Hill and Johnson, 1981; Jensen and Nielsen, 1986; Quintana-Ascencio, González-Espinosa, and Ramírez-Marcial, 1992). It has been argued that the rapid germination (nondormancy) and establishment of white oaks allow escape from postdispersal seed predation, since they permit the seedling to escape seed recovery by caching animals (Barnett, 1977; Fox, 1982). However, the probabilities of survival and continued growth of a seedling after detachment of the acorn (cotyledons) may be affected by the amount of reserves originally available to the seedling. Herbivory, frost, drought, and pathogens are other common challenges facing a seedling early in its life and its ability to cope with them is likely affected by the presence or absence of cotyledons, the size of the seed from which it originated, and the time elapsed since germination.

Although Mexico has the world's greatest oak diversity (around 200 species; Bonfil, 1993; González-Rivera, 1993; Nixon, 1993), very little is known about their ecology. *Quercus rugosa* (subgenus *Leucobalanus*) is a 15–20 m tall tree, widely distributed in Mexico, that frequently coexists with *Q. laurina* (subgenus *Erythrobalanus*), a 15–30 m tall tree (González-Villareal, 1986; Bello and Labat, 1987). Both species are abundant in the

fast-disappearing woodland areas of the hills south and southwest of Mexico City and can be found in pure oak stands or intermingled with pines at higher elevations. Natural regeneration of these species is impeded in this area by predation of germinated acorns and removal of part or all of the shoot by rabbits and small rodents (C. Bonfil, unpublished data), although other factors, such as changes in the disturbance pattern of the stand, may also play a role.

In this study I evaluate the effects of seed size and presence or absence of cotyledonary reserves on survival and growth of seedlings of *Q. rugosa* and *Q. laurina*, in the presence and absence of simulated herbivory. My objectives were to determine (1) whether differences in the ability of 1-mo-old seedlings to survive detachment of cotyledons are related to seed size, (2) whether reserves remaining in the cotyledons at this moment still contribute to survival and further seedling growth, (3) the interaction of herbivory and seed size on seedling survival and growth, and (4) the consequences of cotyledon removal on the response of the seedlings to simulated herbivory.

MATERIALS AND METHODS

During January 1993, acorns were collected from below six different trees each of *Q. rugosa* and *Q. laurina* at an elevation of ~2600 m in the Parque Ecológico de la Ciudad de México in the Ajusco Hills. The sampled trees were all taller than 10 m, with well-developed crowns and located in semi-open forest patches, where it was unlikely that I would find acorns of other trees below the sampled trees. The seeds were floated in water to separate viable seeds from those that were parasitized (mainly by curculionids). Each viable acorn was marked with a number and its individual mass recorded. A subsample ($N = 62$ for *Q. rugosa*, $N = 54$ for *Q. laurina*) was oven dried for 48 h at 80°C and used to evaluate the relationship between fresh and dry mass and the proportion of dry mass attributable to cotyledons. Histograms of fresh mass data of all the seeds (1185 for *Q. rugosa*, 1075 for *Q. laurina*) were used to assign each seed to one of three size categories, small (<1.5 g), medium (1.5–2.5 g for *Q. rugosa*, 1.5–2.0 g for *Q. laurina*), and large (>2.5 g for *Q. rugosa*, >2.0 g for *Q. laurina*) within each species.

In May 1993, the seeds were soaked for 24 h in a 1 g/L giberellic acid solution, which had been shown to synchronize germination in previous trials. Seeds were then placed horizontally on trays containing agrolita (a porous inert material that retains moisture). Every other day the trays were watered and the seeds inspected to record the date of germination, which was defined as the day when the radicle reached 0.5 cm in length.

Two weeks after germination, the agrolita was carefully rinsed off the roots and seedlings were transplanted to black plastic bags (24 cm long, 10 cm diameter, with drainage holes) filled with homogenized soil from the study site. Two weeks later, when seedlings were 1 mo old, each member of a given seed size class was randomly assigned to one of six experimental treatments. This gave a total of 18 treatments, with three factors considered being seed size (small, medium, and large), level of simulated herbivory (0, 50, or 100% of shoot length removed) and removal of cotyledons (presence-absence). These levels of herbivory are frequently observed in nature, and in both cases (50 and 100%) usually entail a complete loss of leaf area, because the young, tender leaves are concentrated on the upper half of the shoot. In this study, the 100% herbivory treatment entailed cutting the shoots 2 cm above the soil.

Cotyledon excision and simulated herbivory were applied simultaneously. The time of treatment application was chosen because previous trials had shown that earlier detachment of cotyledons causes death of

seedlings, and in nature acorn removal is most likely soon after germination, while it is still attractive and nutritious. At this moment all seedlings had completed their first burst of shoot elongation and had expanded leaves, which indicated relative homogeneity of developmental stage among seedlings (Hanson et al., 1986) at the time of treatment, although there was some variation in the completion of leaf elongation.

This design allowed assessment of the impact of shoot removal on survival and growth of seedlings coming from different seed sizes and to evaluate the role played by the remaining cotyledonary reserves in the presence and absence of herbivory. As oak germination is hypogeal there are no confounding effects of any contribution from cotyledonary photosynthesis.

Twenty-five seedlings of *Q. rugosa* were assigned to each of 18 treatment combinations. Due to poor germination, only 17 *Q. laurina* seedlings were available for each treatment. During application of treatments, shoot height and number of leaves were recorded and those seedlings that kept their cotyledons were superficially unearthed and reburied in the same way as those from which cotyledons were removed. The black plastic bags were covered with white plastic bags to avoid excessive heating by the sun and seedlings were placed in a nursery covered with green plastic mesh that provided shade and allowed rainwater to pass through. Seedlings were placed on wire-mesh tables in a completely randomized design, with a border row of extra seedlings around each table to minimize edge effects. Rainfall was supplemented by watering to maintain the soil moist.

Starting on 15 July (3–4 wk after application of treatments), seedling height and total number of leaves were recorded twice a month and the length of each leaf was measured once a month. Total leaf area was estimated by means of a previously developed regression of leaf area vs. leaf length ($r^2 = 0.917$, $N = 93$ for *Q. rugosa* and $r^2 = 0.963$, $N = 183$ for *Q. laurina*). Seedlings were harvested at the end of November 1993, 5 mo after treatments, and total shoot length, basal diameter, and leaf area were measured (leaf area meter, Delta T Devices, Cambridge, UK). Seedlings were oven dried for 48 h at 80°C and each seedling part (root, shoot, and leaves) was individually weighed. The total growth period of 6 mo corresponds to the normal oak growing season at the collection site.

Mean seed masses of the two species were compared by a t test. The relationship between seed fresh and dry mass of each species was examined by regression. Data on survival were analyzed by means of logit analysis for binomial data (i.e., proportions), using the GLIM 3.77 statistical package (Crawley, 1993). By using a logit transformation (p/q; where $q = 1-p$) of p (in this case proportions surviving), the model linearizes the observed values of the proportions and relates each observed value to a predicted value. The latter is obtained by the logit transformation of the value emerging from the linear predictor, which is a linear sum of the effects of one or more explanatory variables.

Data on size of seedlings coming from different seed sizes were compared before treatments were applied by means of a Kruskal-Wallis test. Variables measuring final size and biomass of each seedling part were analyzed by means of ANOVA. MANOVA was used to examine the three biomass response variables (root, shoot, and leaves). When necessary, data were transformed in order to fulfill the requirements of homoscedasticity for the ANOVAs. Relative height growth rates (RGR) were analyzed to control for differences at the moment of treatment application.

RESULTS

Seed mass—The two species differed significantly ($t = 6.25$, $P < 0.001$, $N = 1185$ for *Q. rugosa*, $N = 1075$ for *Q. laurina*) in their mean seed masses. Although the magnitude of the difference was small, the range of variation of seed sizes was quite different in the two species (Fig. 1, mean = 1.99 g, SD = 1.14 for *Q. rugosa* and mean = 1.75 g, SD = 0.48 for *Q. laurina*). There was a
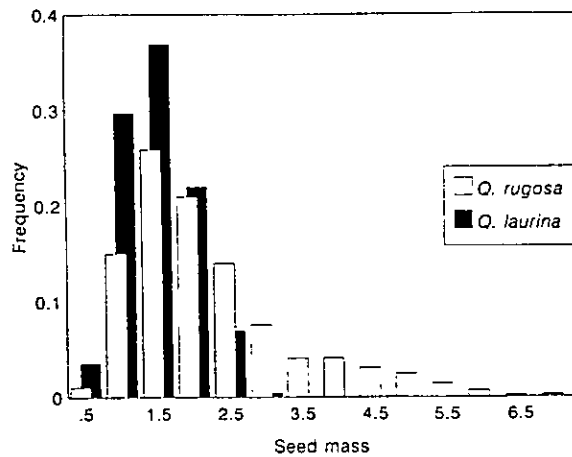
Fig 1. Frequency distributions of fresh seed mass classes of *Q. rugosa* and *Q. laurina.*

strong correlation between acorn fresh and dry masses for both species ($r^2 = 0.998$ for *Q. rugosa*, $r^2 = 0.997$ for *Q. laurina*), as well as between total fresh mass and cotyledon dry mass ($r^2 = 0.995$ for *Q. rugosa*, $r^2 = 0.992$ for *Q. laurina*), allowing me to consider seed fresh mass as a good indicator of the amount of reserves available for seedling growth. Additionally, it has been shown in other oaks that there are high correlations between seed size and contents of ash, energy, and storage compounds (Triphati and Kahn, 1990). The embryo (including cotyledons) accounted for a high proportion of total seed dry mass (53–75% for *Q. rugosa*, 53–68% for *Q. laurina*).

Seedling survival—Seed size had a clear effect on survival of *Q. rugosa*, with seedlings from large seeds having the highest and seedlings from small seeds the lowest survival (Table 1). Within each size class, survival was lowered by removal of the cotyledons and by increasing levels of shoot removal. The effects of cotyledon removal, seed size, and herbivory were highly significant ($P \leq 0.001$ for all three cases), and the interactions between these variables were not ($P > 0.4$ in all cases).

It is necessary to note here that, because logistic models are bounded by zero and one, the effect of a given change of the independent variable on the dependent variable (probability of survival) is nonlinear, increasing when the values of the dependent variable are most distant from their upper and lower asymptotes (zero and one, respectively). Accordingly, the fitted logistic model predicts a quantitatively larger effect of cotyledon removal on small-seeded seedlings, where survival is expected to drop 17% (from 0.98 to 0.81) as a result of the removal, while the predicted drop in large-seeded seedlings is only 0.8% (from 0.999 to 0.991). Likewise, the effect of the highest level of herbivory was quantitatively larger on small-seeded seedlings, where survival drops 13% as a result of biomass removal, while the drop in large-seeded seedlings is only 0.6% (Table 1). Thus, in spite of the absence of statistically significant interactions in the logistic model, the biological effects of both herbivory and cotyledon removal display a strong synergism in small-seeded seedlings.

TABLE 1. Survival (proportion) of *Quercus rugosa* and *Quercus laurina* seedlings in the presence and absence of cotyledons (+/− cot.) at three levels of simulated herbivory. The numbers in parentheses indicate the expected values of the logistic model. Since herbivory did not have a significant effect in *Q. laurina*, the expected values are the same for all three herbivory levels.

Herbivory (%)	Seed size					
	Small		Medium		Large	
	+ cot.	− cot.	+ cot.	− cot.	+ cot.	− cot.
	Quercus rugosa					
0	1.00	0.81	1.00	0.95	1.00	0.96
	(0.979)	(0.81)	(0.994)	(0.944)	(0.999)	(0.991)
50	0.91	0.52	1.00	0.73	1.00	1.00
	(0.917)	(0.507)	(0.978)	(0.803)	(0.997)	(0.965)
100	0.80	0.36	0.95	0.71	1.00	0.92
	(0.847)	(0.339)	(0.956)	(0.671)	(0.993)	(0.933)
	Quercus laurina					
0	0.75	0.22	0.69	0.23	0.83	0.35
50	0.85	0.21	0.67	0.07	0.83	0.06
100	0.50	0.11	0.56	0.00	0.95	0.06
	(0.74)	(0.139)	(0.646)	(0.094)	(0.823)	(0.209)

In contrast to *Q. rugosa*, cotyledon loss caused greater mortality in *Q. laurina* and seed size did not compensate for this loss (Table 1). The effects of seed size ($P = 0.052$) and cotyledon removal ($P < 0.001$) were significant, with the predicted drop in survival due to cotyledon loss 60% in both large and small-seeded seedlings (Table 1). Herbivory ($P = 0.12$) and the interactions among variables were not significant (size × herbivory $P = 0.31$; size × cotyledon $P = 0.24$; herbivory × cotyledon, $P = 0.08$). Results for *Q. laurina* must, however, be treated with caution because some seeds and seedlings showed evidence of pathogen attack (probably a fungus), reducing survival even in seedlings from the control group. Most mortality in both species occurred during the 1st mo after the application of treatments and those seedlings unable to resprout after 4 wk soon died.

Seedling growth—Quercus rugosa—The effect of seed size on height was evident throughout the growing season, regardless of the level of herbivory. At the moment of application of treatments, there were already significant differences in height (Kruskal-Wallis $H = 14.45$, $P = 0.007$) and number of leaves ($H = 19.37, P = 0.001$) between seedlings coming from different seed sizes. Leaf development was greater in seedlings from medium and large seeds (median = 5 leaves) than from small seeds (median = 3 leaves).

Herbivory, as expected, resulted in a pronounced reduction in height in all cases, and seedling height was further reduced by the removal of cotyledons. Without herbivory, loss of cotyledons did not have a very pronounced effect on height, except for a small reduction in seedlings from small seeds. In seedlings with cotyledons, height was similar between those that lost 50 and 100% of their shoot, but differences between these herbivory levels were greater in seedlings from small and medium seeds without cotyledons (Fig. 2A-C).

Seed size, herbivory, and cotyledons, as well as all second-order interactions, had a significant effect on

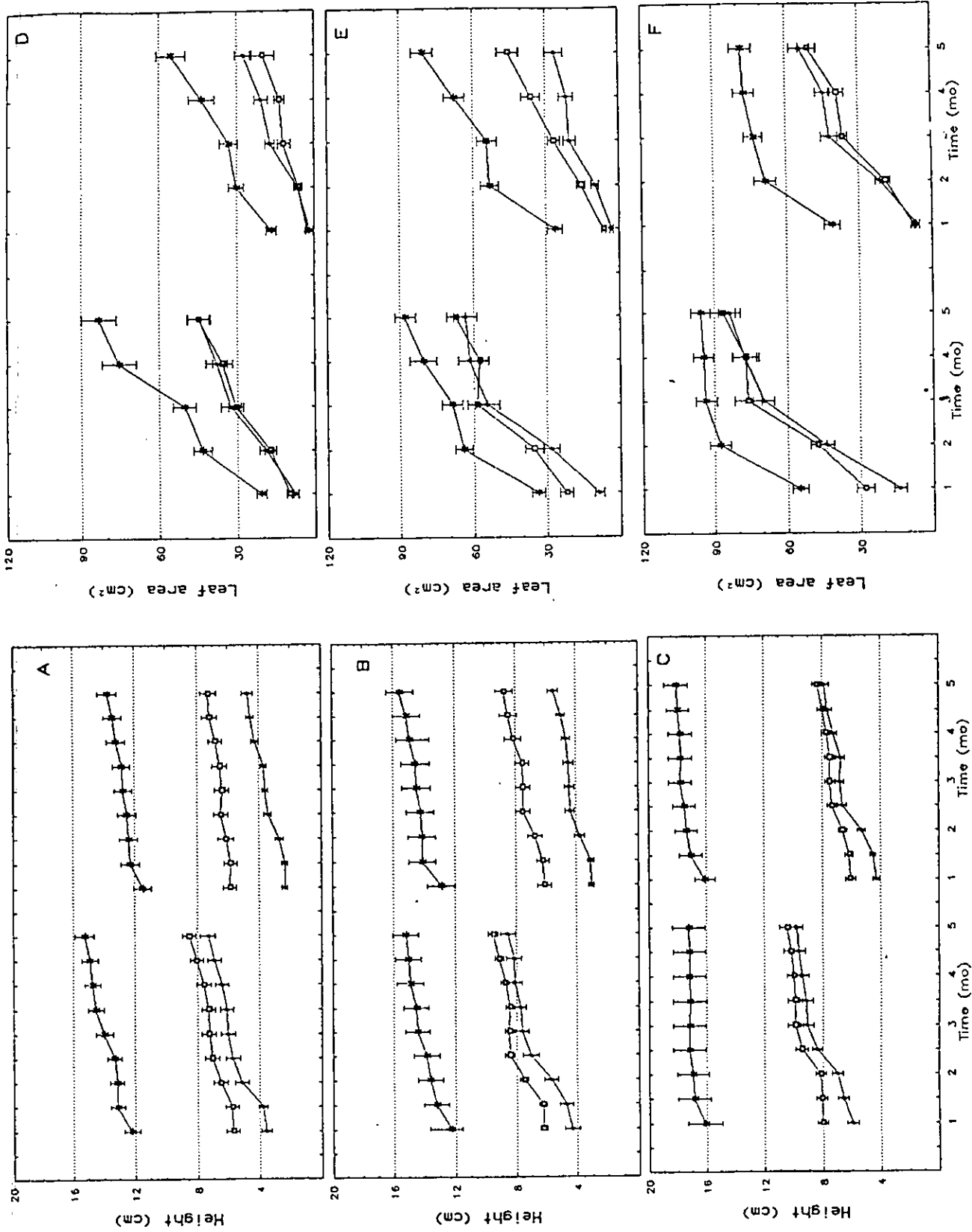Fig. 2. Height and leaf area ($\bar{X} \pm 1$ SE) of seedlings of *Q. rugosa* 1–5 mo after application of treatments. (A, D) Small-seeded seedlings; (B, E) medium-seeded seedlings; and (C, F) large-seeded seedlings. Within each box, the left side corresponds to seedlings with cotyledons and the right side to those without. Herbivory: asterisks, 0%; unfilled squares, 50%, and filled diamonds, 100% of shoot height.

TABLE 2. ANOVAs on relative growth rates.

Effect	F	df	P
Q. rugosa			
Size	12.28	2	<0.001
Herbivory	792.57	1	<0.001
Cotyledons	59.65	1	<0.001
Size × Herb.	8.65	2	<0.001
Size × Cot.	4.34	2	0.014
Herb × Cot.	15.79	1	<0.001
S × H × C.	1.76	2	0.173
Error		215	
Q. laurina			
Size	1.03	2	0.362
Herbivory	59.95	1	<0.001
Size × Herb.	0.29	2	0.747
Error		62	

RGR (Table 2). This analysis excluded seedlings without herbivory, due to differences in variability in the response of seedlings with and without herbivory. In general, seedlings with 100% herbivory had higher RGRs than those with 50%, and RGRs increased with seed size. The lack of cotyledons caused a reduction in RGRs in all cases, although this reduction was smaller in seedlings from large seeds. Differences between seedlings with and without cotyledons were more pronounced in the 100% herbivory treatment than in the 50% shoot loss.

There was a highly significant effect of the three factors on final shoot height, leaf area, basal diameter, number of leaves, and mean area per leaf (Table 3). The herbivory × cotyledon interaction was significant for almost all of them, due to the fact that the effect of increasing levels of herbivory was amplified by the absence of cotyledons. The seed size × herbivory interaction was significant in some cases, while the seed size × cotyledon interaction was not in most cases. The third-order interaction, significant in two cases, is difficult to interpret.

The conspicuous effect of herbivory on shoot height persisted until the end of the experiment, with seedlings that suffered 100% herbivory half the final height of those without herbivory. It also reduced leaf area in all seed sizes, although little difference was observed between 50% and 100% herbivory (Fig. 2D-E). In large-seeded seedlings that kept their cotyledons there was a noticeable recovery in leaf area towards the end of the growing season. The effects of herbivory were always

mitigated by the presence of cotyledons, with 50–150% more final leaf area relative to seedlings without cotyledons.

Cotyledon retention had the largest influence on both total leaf area and mean area per leaf, while herbivory affected total leaf area more than individual leaf area. Seedlings that suffered herbivory and lost their cotyledons generally had the fewest leaves. Herbivory caused a greater reduction in the diameter of seedlings coming from small seeds than from the other seed size classes.

MANOVA showed that the three variables studied had highly significant effects on the biomass (dry mass) of the various seedling parts ($P < 0.0001$). ANOVAs were then carried out to analyze their effects on the biomass of each seedling organ (Table 3), with all three variables having a significant effect on total, root, shoot, and leaf dry mass. In all cases, the most conspicuous effect was due to cotyledon retention, followed by herbivory and seed size. The seed size × herbivory interaction was significant in all cases, due to the greater impact herbivory had on dry mass of small-seeded seedlings. Mean total dry mass responded in a manner similar to that of seedling parts. In general, the two levels of herbivory had a similar effect, but were clearly different from the control group (Fig. 3). There was also a trend for the effect of cotyledon retention to be more conspicuous when herbivory occurred.

The proportion of dry mass accounted for by the root (root mass ratio) in seedlings that did not experience herbivory differed significantly with seed size (small = 0.47, medium = 0.48, large = 0.53, $F = 5.2$, df = 2, 81; $P = 0.007$). The presence or absence of cotyledons did not affect this relationship.

Quercus laurina—The low number of seedlings surviving in treatments where cotyledons were detached did not allow a sound comparison between the growth parameters of seedlings with and without cotyledons, so comparisons were made only among those treatments with cotyledons. As with *Q. rugosa*, 1 mo after germination there were already significant differences in height (Kruskal-Wallis $H = 12.39$, $P = 0.002$) and leaf number (Kruskal-Wallis $H = 7.48$, $P = 0.24$) among seedlings from small, medium, and large seeds.

Differences in height due to herbivory were maintained in seedlings of the three size classes throughout

TABLE 3. *Quercus rugosa*: F statistics and probabilities for ANOVAs.

Variable	Seed size F	Seed size P	Herbivory F	Herbivory P	Cotyledons F	Cotyledons P	Size × Herb. F	Size × Herb. P	Size × Cot. F	Size × Cot. P	Herb × Cot. F	Herb × Cot. P	S × H × C F	S × H × C P
df treatment[a]	df 2		df 2		df 1		df 4		df 2		df 2		df 4	
Shoot height	22.81	<0.00001	274.75	<0.00001	98.32	<0.00001	1.01	NS	3.45	0.033	6.46	0.002	2.50	0.043
Leaf area	28.76	<0.00001	63.86	<0.00001	97.56	<0.00001	2.31	NS	0.27	NS	3.72	0.03	1.86	NS
Diameter	69.36	<0.00001	111.45	<0.00001	139.78	<0.00001	5.03	0.006	0.96	NS	0.35	NS	3.32	0.01
No. leaves	3.89	0.02	33.47	<0.00001	7.46	0.007	6.81	0.00003	2.44	NS	6.93	0.001	2.07	NS
Mean area per leaf	31.86	<0.00001	17.72	<0.00001	96.09	<0.00001	0.72	NS	0.31	NS	3.44	0.03	1.89	NS
Biomass														
Shoot	86.83	<0.00001	186.45	<0.00001	251.25	<0.00001	2.68	0.03	0.89	NS	5.50	0.005	4.38	0.002
Leaves	48.97	<0.00001	70.57	<0.00001	141.89	<0.00001	4.39	0.002	0.26	NS	4.06	0.02	3.24	0.01
Root	90.49	<0.00001	86.60	<0.00001	145.76	<0.0001	4.37	0.002	0.48	NS	6.01	NS	3.12	0.02
Total	101.41	<0.001	123.25	<0.00001	219.18	<0.00001	6.12	0.001	0.89	NS	10.34	0.00005	4.68	0.043

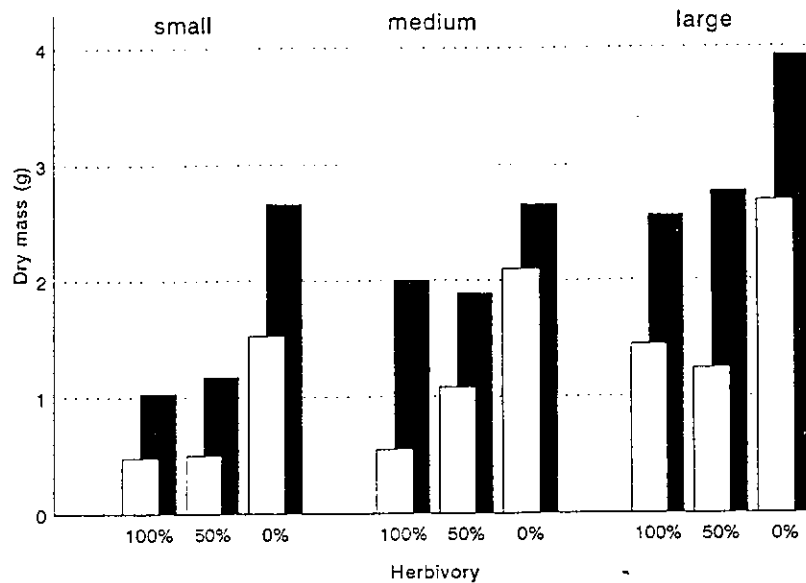[a] df error: 235 for size variables, 233 for biomass variables.

Fig. 3. Total dry mass of seedlings of *Q. rugosa*. Back, seedlings with cotyledons; front, seedlings without them.

the growing season. Relative height growth rates were not significantly affected by seed size nor by the seed size × herbivory interaction (Table 2; Fig. 4A-C). The growth plots for seedlings without cotyledons, although produced with small sample sizes, suggest that cotyledon loss had a great impact on both seedling height and leaf area, as was the case for *Q. rugosa* (Fig. 4C, F). Due to a high variability of shoot height in this species, the homoscedasticity requirement could not be fulfilled and this variable was not analyzed by ANOVA.

Final leaf area and basal diameter were both significantly affected by seed size and herbivory (Table 4, Fig. 4). Total number of leaves was significantly affected by seed size, while mean area per leaf was affected by herbivory. Seedlings from large seeds had an average of 3.5 more leaves than seedlings from small- or medium-sized seeds and those without herbivory had larger leaves.

MANOVA of biomass data of the various seedlings parts showed a significant effect of both seed size and herbivory ($P < 0.0001$). The individual ANOVAs showed that, with the exception of shoot mass, seed size was more important than herbivory in the biomass attained at the end of the season, although both variables had significant effects on almost every seedling part (Table 4). The strong effect of herbivory on shoot mass, as on height, indicates that seedlings are unable to recover from loss of aerial tissue in one growing season.

Seedlings from large seeds had a clear advantage in most cases, while there were not always differences between seedlings from small- and medium-sized seeds. Herbivory resulted in a clear decrease in total dry mass. Seed size did not have a significant effect on root mass ratio in this species.

DISCUSSION

Differences among species in average seed mass were relatively small, but the results agree with the reported tendency for white oaks (subgenus *Leucobalanus*) to have larger seed sizes than red oaks (subgenus *Erythro-*

balanus) (Sork, 1993). The variation in seed size found in *Q. rugosa* was large, even though only within-population variation was examined. In the Ajusco Hills, this species has a wide distribution, whereas *Q. laurina* occupies more protected, humid sites with well-developed soils. The variation in seed size may give *Q. rugosa* the ability to establish in a mosaic of microsites with different physical and biotic conditions, thus broadening its regeneration niche (sensu Grubb, 1977).

Survival was greatly reduced by cotyledon removal in both species, demonstrating that the reserves remaining in the seed 1 mo after germination still contribute to seedling survival. Survival after cotyledon excision was higher in *Q. rugosa* than in *Q. laurina*, indicating a more extended dependence on these reserves in the latter.

My results have implications for the hypothesis of nondormancy as a means of escaping postdispersal seed predation, as the probabilities of surviving cotyledon detachment are significantly higher in large-seeded seedlings. Predators would prefer to excise the cotyledon as early as possible, before its food reserves are consumed by the seedling. However, early excision of the acorn greatly reduces the chances of a successful escape. For the species considered here, previous trials showed that seedlings are unable to survive if cotyledons are removed 7-15 d after germination (C. Bonfil, unpublished data). For most species, we do not know the time required to attain complete independence from cotyledonary reserves, both in terms of survival and growth, a factor that could have ecological relevance.

In both species there is a clear effect of seed size on seedling growth, both initially and at the end of the growing season. In *Q. rugosa* the effects of seed size and cotyledon retention become more important when seedlings suffer herbivory. Higher relative height growth rates are associated with cotyledon retention, and the consistent increase in RGRs with seed size both in seedlings with and without cotyledons shows the importance of having a large supply of reserves at germination.

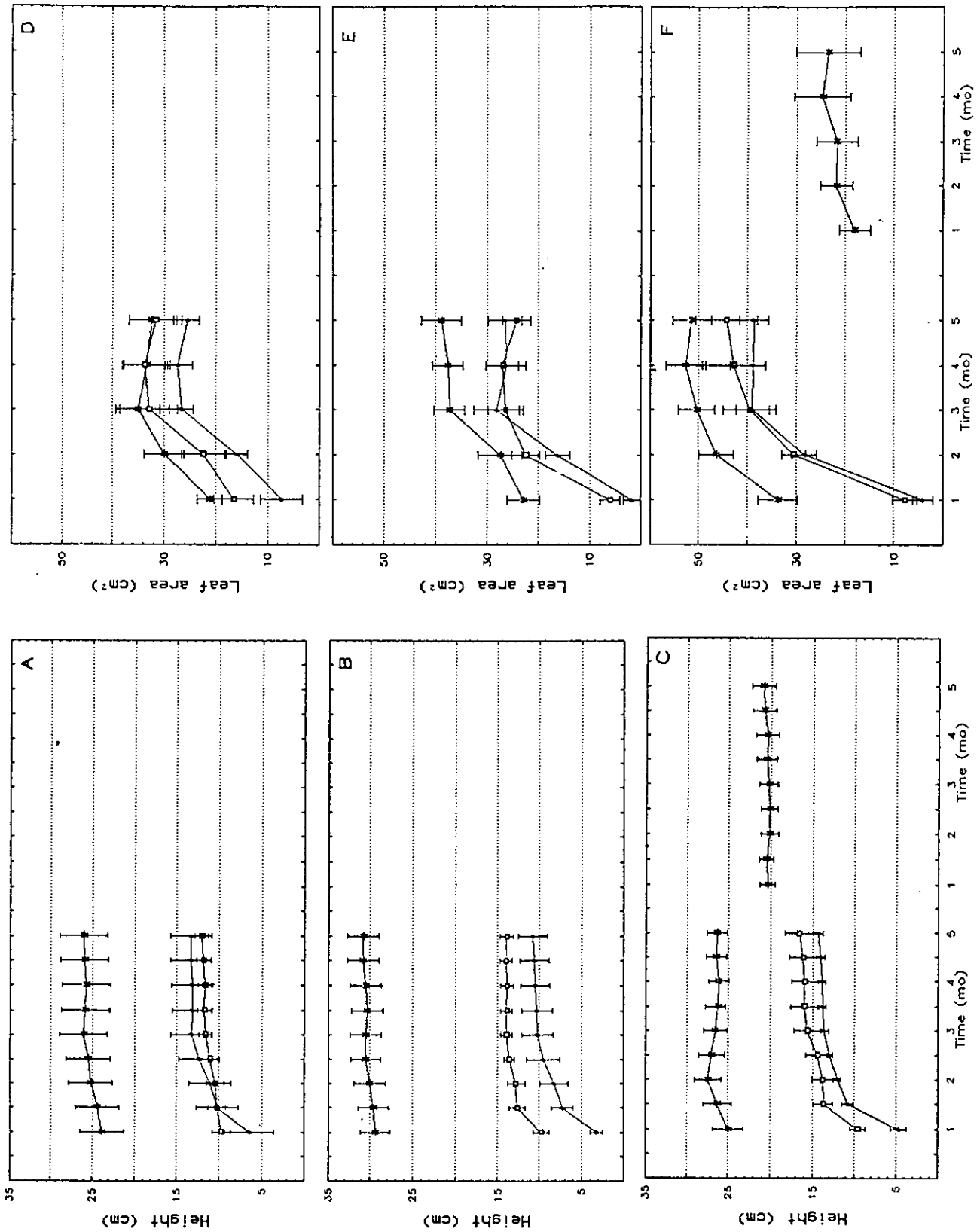Fig. 4. Height and leaf area ($\bar{X} \pm 1$ SE) of seedlings of *Q. laurina* 1–5 mo after application of treatments. (A, D) Small-seeded seedlings; (B, E) medium-seeded seedlings; and (C, F) large-seeded seedlings. Within each box, the left side corresponds to seedlings with cotyledons and the right side lines to seedlings without. Herbivory: asterisks, 0%; unfilled squares, 50%; and filled diamonds, 100% of shoot height.

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TABLE 4. *Quercus laurina*: *F* statistics and probabilities for ANOVAs.

Variable	Seed size		Herbivory		Size × Herb.	
	F	P	F	P	F	P
df treatment[a]	df 2		df 2		df 4	
Leaf area	9.97	0.0001	4.14	0.02	1.89	NS
Diameter	7.25	0.001	4.43	0.015	1.56	NS
No. leaves	3.78	0.03	0.57	NS	0.89	NS
Mean area per leaf	2.10	NS	4.14	0.02	0.55	NS
Biomass						
Shoot	18.22	<0.00001	42.27	<0.00001	2.19	NS
Leaves	12.76	0.00002	4.02	0.02	1.00	NS
Root	19.98	<0.00001	1.99	NS	1.22	NS
Total	26.09	<0.0001	15.11	<0.00001	1.94	NS

[a] df error: 77.

The removal of 50% of the shoot resulted in the loss of most leaves and frequently produced shoot dieback. This, combined with the higher subsequent RGR of plants in the 100% shoot loss treatment, resulted in both levels of herbivory having similar final sizes and biomasses (Figs. 2–4). In nature, total removal of the shoot by herbivores is more frequent. Growth was generally reinitiated from lower buds, often resulting in the development of two new branches. This pattern is common in oak seedlings (Crow, 1988) and branches of oak trees (Heichel and Turner, 1984), which form more lateral branches as a result of defoliation (Hilton et al., 1987).

In *Q. laurina*, seed size significantly affected seedling sizes 1 and 6 mo after germination, weakly affected survival, and did not affect RGR between 1 and 6 mo. This suggests that differences among seed size classes in height at 6 mo are determined principally in the 1st mo.

The relationship between seed and seedling size in oaks has been described before (McComb, 1934; Triphati and Kahn, 1990; Tecklin and McCreary, 1991). My study shows that in *Q. rugosa* the capacity of seedlings to recover from herbivory is mediated by seed size, since the decrease in number of leaves, diameter, and total dry mass of seedlings that suffered herbivory diminished with increasing seed size. Nevertheless, differences in height and biomass between uncut seedlings and those that suffered artificial herbivory were maintained until the end of the study period. Welker and Menke (1990) also found that severely defoliated *Quercus douglasii* seedlings did not accumulate biomass to levels that approached non-defoliated seedlings.

The fact that seed size has an effect even when cotyledons are excised shows that 1 mo after germination, differences in supply are already evident and have important consequences for the seedlings. This reinforces the view that in oaks the seed reserves are quickly directed to the root (McComb, 1934; Grime and Jeffrey, 1965), where they remain available for seedling resprout (Matzuda and McBride, 1986; Crow, 1988; Walters, Kruger and Reich, 1993) after disturbance-caused death of aerial biomass. The positive relationship found between seed size and root mass ratio also supports this idea, although it was found only in *Q. rugosa*. In this species root biomass was reduced by herbivory, a fact that may reflect the utilization of stored reserves in the production of a new shoot. Parker and Patton (1975) found that de-

foliation of *Quercus velutina* seedlings caused a depletion of the starch reserves in the roots.

In an environment where the aerial biomass of young oak seedlings is frequently lost due to the action of herbivores and/or harsh climatic conditions, seed size plays an important role in determining which individuals will prevail. However, given the large intrapopulation variation in seed size, other ecological factors, such as dispersal, seed predation, and water relations may confer an advantage to different seed sizes (Stanton, 1985). Safe-site requirements could also differ for seeds of different sizes. The study of different groups of species would yield important insights into the adaptive significance of seed size in diverse ecological contexts and also help to evaluate the relative contributions of historic and ecological factors to the responses observed.

LITERATURE CITED

ARMSTRONG, D. P., AND M. WESTOBY. 1993. Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. *Ecology* 74: 1092–1100.

BAKER, H. G. 1972. Seed weight in relation to environmental conditions in California. *Ecology* 53: 997–1010.

BARNETT, R. J. 1977. The effect of burial by squirrels on germination and survival of oak and hickory nuts. *American Midland Naturalist* 98: 319–330.

BELLO GONZÁLEZ, M. A., AND J. N. LABAT. 1987. Los encinos (*Quercus*) del estado de Michoacán, México. SARH, CEMCA. Cuadernos de Estudios Michoacanos 1.

BONFIL, C. 1993. La riqueza de los encinos. *Ciencias* 29: 13–15.

CRAWLEY, M.J. 1993. GLIM for ecologists. Blackwell Scientific Publications, London.

CROW, T. R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—a review. *Forest Science* 34: 19–40

DARLEY-HILL, S., AND W. C. JOHNSON. 1981. Acorn dispersal by the Blue Jay (*Cyanocitta cristata*). *Oecologia* 50: 231–232.

FOSTER, S. A. 1986. On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Botanical Review* 52: 260–299.

———, AND C. H. JANSON. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 66: 773–780.

FOX, J. F. 1982. Adaptation of gray squirrel behavior to autumn germination by white oak acorns. *Evolution* 36: 800–809.

GONZÁLEZ-RIVERA, R. 1993. La diversidad de los encinos mexicanos. *Revista de la Sociedad Mexicana de Historia Natural* Vol. Esp. (XLIV): 125–142.

GONZÁLEZ-VILLAREAL, L. M. 1986. Contribución al conocimiento del

género *Quercus* (*Fagaceae*) en el estado de Jalisco. Instituto de Botánica. Univ. de Guadalajara. Colección Flora de Jalisco.

GRIME, J. P., AND D. W. JEFFREY. 1965. Seedling establishment in vertical gradients of sunlight. *Journal of Ecology* 53: 621–642

GROSS. K. L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology* 72: 369–387.

GRUBB. P. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review* 52: 107–145.

HANSON, P. J., ET AL. 1986. A morphological index of *Quercus* seedling ontogeny for use in studies of physiology and growth. *Tree Physiology* 2:273–281.

HEICHEL. G. H., AND N. C. TURNER. 1984. Branch growth and leaf numbers of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): response to defoliation. *Oecologia* 62: 1–6.

HILTON. G. M., J. R. PACKHAM, AND A. J. WILLIS. 1987. Effects of experimental defoliation on a population of pedunculate oak (*Quercus robur* L.). *New Phytologist* 107: 603–612.

JENSEN. T. S., AND O. F. NIELSEN. 1986. Rodents as seed dispersers in a heath-oak wood succession. *Oecologia* 70: 214–221.

KELLY. C. K., AND A. PURVIS. 1993. Seed size and establishment conditions in tropical trees. *Oecologia* 94: 356–360.

LEISHMAN, M. R., AND M. WESTOBY. 1994. The role of large seed size in shaded conditions: experimental evidence. *Functional Ecology* 8: 205–214.

MATZUDA. K., AND J. R. McBRIDE. 1986. Difference in seedling growth morphology as a factor in the distribution of three oaks in central California. *Madroño* 33: 207–216.

MAZER. S. J. 1989. Ecological, taxonomic and life history correlates of seed mass among Indiana dune angiosperms. *Ecological Monographs* 59: 153–175.

McCOMB. A. L. 1934. The relation between acorn weight and the development of one year chestnut oak seedlings. *Journal of Forestry* 32: 479–484.

McWILLIAMS. E. L., R. Q. LANDERS, AND J. P. MAHLSTEDE. 1968. Variation in seed weight and germination in populations of *Amaranthus retroflexus* L. *Ecology* 49: 290–296

MELLANBY. K. 1968. The effects of some mammals and birds on regeneration of oak. *Journal of Applied Ecology* 5: 359–366.

NIXON. K. C. 1993. The genus *Quercus* in Mexico. *In* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa [eds.], Biological diversity of Mexico: origins and distribution. 439–458. Oxford University Press, Oxford.

PARKER. J., AND R. L. PATTON. 1975. Effects of drought and defoliation on some metabolites in roots of black oak seedlings. *Canadian Journal of Forest Research* 5: 457–463.

QUINTANA-ASCENCIO. P., M. GONZÁLEZ-ESPINOSA, AND N. RAMÍREZ MARCIAL. 1992. Acorn removal, seedling survivorship, and seedling growth of *Quercus crispipilis* in succesional forests of the high-

lands of Chiapas, Mexico. *Bulletin of the Torrey Botanical Club* 119: 6–18.

SALISBURY. E. J. 1942. The reproductive capacity of plants. G. Bell and Sons. London.

———. 1974. Seed size and mass in relation to environment. *Proceedings of the Royal Society of London* B186: 83–88.

SCHIMPF. D. J. 1977. Seed weight of *Amaranthus retroflexus* in relation to moisture and length of growing season. *Ecology* 58: 450–453.

SEIWA. K., AND K. KIKUZAWA. 1991. Phenology of tree seedlings in relation to seed size. *Canadian Journal of Botany* 69: 532–538.

SHAW. M. W. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petrae*) in North Wales. II. Acorn losses and germination under field conditions. *Journal of Ecology* 56: 565–583.

SORK. V. L. 1993. Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp). *Vegetatio* 107/108: 133–147.

STANTON. M. 1984. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65: 1105–1112.

———. 1985. Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum* L.): the establishment of a fitness hierarchy. *Oecologia* 67: 524–531.

TECKLIN. J., AND D. D. McCREARY. 1991. Acorn size as a factor in early seedling growth of blue oak. USDA Forest Service General Technical Report PSW-126: 48–53.

TRIPATHI. R. S., AND M. L. KAHN. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet forest. *Oikos* 57: 289–296.

WALTERS. M. B., E. L. KRUGER, AND P. B. REICH. 1993. Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. *Oecologia* 94: 7–16.

WELKER. J. M., AND J. W. MENKE. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook and Arn.) seedlings under slow and rapid rates of soil drought. *Functional Ecology* 4: 807–817.

WELLER. S. J. 1985. Establishment of *Lithospermum carolinense* on sand dunes: the role of nutlet mass. *Ecology* 66: 1893–1901.

WEIS. Y. M. 1982. The effects of propagule size on germination and seedling growth in *Mirabilis hirsuta*. *Canadian Journal of Botany* 60: 1868–1874.

WERNER. P. A., AND W. J. PLATT. 1976. Ecological relationships of cooccurring goldenrods (*Solidago:Compositae*). *American Naturalist* 110: 959–971.

WESTOBY. M., E. JURADO, AND M. LEISHMAN. 1992. Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution* 7: 368–372.

WINN. A. A. 1985. Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. *Journal of Ecology* 73: 831–840.

WULFF. R. D. 1986. Seed size variation in *Desmodium paniculatum* II. Effects on seedling growth and physiological performance. *Journal of Ecology* 74: 99–114.

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CAPÍTULO   III

Dinámica de plántulas de *Quercus rugosa*

como una herramienta para su

reintroducción en un

paisaje perturbado
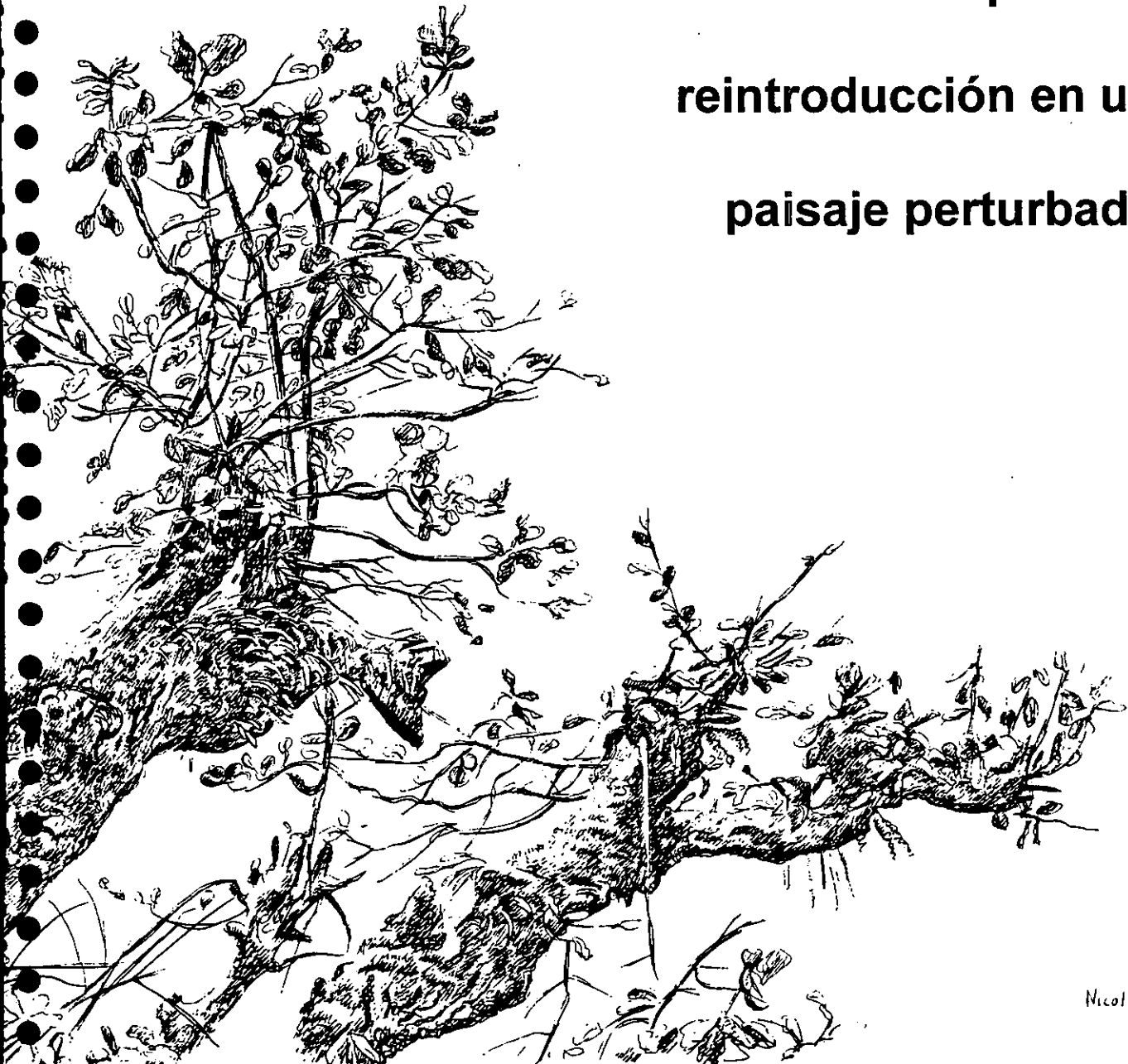
Nicolas Moreno
1986

Seedling dynamics of *Quercus rugosa* as a tool for its

reintroduction

in a disturbed landscape

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Abstract

Seed predation and germination, as well as seedling survival and growth of *Quercus rugosa* were studied in three different sites (the forest interior, the forest border and a disturbed site) along a disturbance gradient, in order to obtain information to define its "regeneration niche" and thus facilitate its reintroduction in a disturbed area.

Acorn removal on the ground was high on the three sites, with higher removal rates on 25-seed density clusters than on 5 and 1-seed clusters. More seeds were removed at the forest border than at the other two sites, although in all cases some seeds remained in the ground for periods long enough for them to germinate and produce seedlings. Without predation, seed germination and seedling establishment were more successful and similar in the forest interior and the forest border, and much lower at the disturbed site, due to acorn desiccation.

Seedling survival was strongly affected by site, with highest survival in the forest border and lowest survival at the disturbed site after a year. The following dry season, which was particularly harsh, caused a drop in survival both at the forest border and the disturbed site. In the former, a closer analysis revealed that partially shaded microsites enhanced survival, while in the latter overall survival was very low at the end of this period, with approximately 5 % of the seedlings alive, compared to 50% survival at the other sites. There was a positive correlation between seed size and seedling survival at the forest border.

The three size variables measured (seedling height, basal diameter and crown area) did not increase noticeably during the 20 mo study period at the forest interior, while there was a noticeable growth at the forest border and the disturbed site. However, during the two dry seasons there were large drops in mean seedling height an crown area at the disturbed site, due to more frequent dieback, causing large variation in seedling size.

The above results show that extensive reintroduction of this species to the disturbed area will probably fail under present conditions, and that careful selection or duplication of microsites that mimic the partial shade of the forest border is a more sound method to improve regeneration at this site.

key words: *Quercus*, regeneration, seed predation, seedling survival and growth, resprouting, population reestablishment.

Introduction

Oaks are dominant elements in many forests, but their regeneration has often proved difficult (Carvell & Tyron 1961, Griffin 1971, Crow 1988, Lathrop and Osborne 1990). Mexico has a great diversity of oaks (between 130 and 200 species, Zavala 1990, Nixon 1993), many of which occupy areas particularly well suited to human settlement and agriculture (Rzedowski 1981). On the low portions of the hills surrounding the Mexico City basin, oak forests are disappearing at a high rate and those that remain suffer the impact of increasing human disturbance (Ezcurra 1990, Aragón 1993). Unfortunately, very little is known about the ecology of these forests. In particular, we need to know the requirements for establishment and growth of the different oak species (Grubb 1977), in order to achieve its successful reintroduction when developing ecological restoration programs in the disturbed areas that are now under protection.

This study analyses the establishment, survival and growth of seedlings of *Quercus rugosa* in three different sites along an environmental gradient created by various disturbance events. Knowledge of seedling dynamics in these three contrasting patches will help to define "safe sites" (Harper 1977, Crow 1992) for the species, facilitating its regeneration in the area. The questions addressed are: a) does acorn predation limit seedling recruitment?, b) does germination and seedling establishment vary along the disturbance gradient?, c) are seedling death causes related to the environment they occupy?, d) what microsite conditions are suitable for seedling survival and growth?, and e) is there an effect of seed size on seedling survival?

Methods

Study site

The study site is located in the Parque Ecológico de la Ciudad de México, a recently protected area in the piedmont of the Ajusco hills, south of Mexico City at an altitude of 2500-2800 m. Mean annual temperature is 15 °C and more than 80% of the annual precipitation of 1000 mm falls from May to October (Alvarez Cruz 1992). Part of this area was covered by lava flowing from the nearby Xitle cone around 2 000 years ago (Cordova et al. 1994), resulting in scattered patches of older, well developed soil, within a matrix of basaltic rock with a poorly developed soil, located mainly in small crevices.

The vegetation is closely related to edaphic conditions, with patches of closed forest dominated by Q. rugosa and Q. laurina found on the portions with deep soil, and a xerophitic shrub vegetation (matorral), dominated by sparse trees of Q. rugosa and occasionally Q. castanea, on the rock bed. A part of this shrubland was severely disturbed in 1987-88 by a temporary human settlement, which removed the substrate in order to use rocks for building huts and fences and left the area almost completely devoid of vegetation (Bonfil et al 1997).

The species

Quercus rugosa adult trees (Lepidobalanus) are 10-20 m high and have gross, rigid leaves, which are partially shed between October an December. Young leaves are produced during February and March, while some old leaves still remain attached to the tree. Acorn fall occurs from October to December and is simultaneous with leaf abscission.

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Site characterization

Seedling establishment and growth were studied in a) the forest interior, with little understory vegetation, b) the forest border, with a sparse tree cover and rich herbaceous and shrub vegetation, and c) the disturbed site, located in the former shrubland, which is now dominated by herbaceous vegetation with some shrubs and young trees of *Buddleia cordata*. All three sites are located on 15-25° slopes facing NE.

At each site the superficial structure of the soil was assessed in twelve 1 x 1 m quadrats chosen at random along a 200 m transect. A metal needle was dropped five times at random in each quadrat and the point of impact was classified as bare volcanic rock, volcanic rock with mosses or lichens, volcanic rock with mosses or lichens and some soil, rock surrounded by soil, well developed soil without rocks, or well developed soil covered by litter.

Three maximum-minimum thermometers were placed approximately 30 cm above the ground at random points on each site and temperature data were recorded weekly throughout 1992. Photosynthetically active radiation (PAR) was measured simultaneously at the three sites using portable radiometers (Li-Cor 185) and quantum sensors, and the radiation reaching ten randomly selected points 10 cm above the ground was recorded every hour on one clear day each month, during six months. Precipitation data were obtained from the nearest operating weather station, approximately 8 Km from the site.

Seed predation and seedling establishment

During October and November 1991 acorns were collected from the study site and tested for viability by floating them in water. Sound acorns were used to evaluate seed removal by predators on the ground. Ten replicas of each of three seed densities (1, 5 and 25 acorns) were placed on the ground at random points along a transect in each site at the beginning of March 1992

and the numbers of acorns remaining were recorded daily for the first week and weekly thereafter until the end of April.

In order to study seed germination and seedling establishment, twelve cages (25 x 30 x 30 cm) of 12 mm wire mesh, painted to avoid oxidation, were fixed to the soil at points chosen at random along a transect. In March 1992, ten acorns were placed inside each cage and covered with the litter present in the surface to mimic natural conditions. The cages were observed monthly to record seedling emergence and they were opened at the end of August to check the condition of the remaining seeds and seedlings.

Seedling survival and growth

Seedlings produced in a local nursery from acorns collected in the area were used to study seedling survival and growth at each site. The seeds were previously tested for viability, numbered, and assigned to small (< 1.5 g), medium (1.5-2.5g), or large (>2.5g) size categories, as previous experiments had shown that seed size affects seedling performance in this species under controlled conditions (Bonfil, 1998). The acorns were germinated in trays containing agrolita, a porous inert material that retains moisture. When the seedlings were approximately 10 cm tall and the first flush of growth was completed (around six months after germination), the agrolita was carefully rinsed away and seedlings were placed in black plastic bags filled with soil from the study site. In the second week of July 1991, approximately 100 seedlings were transplanted to each site at randomly chosen points along transects with a fixed orientation. There were approximately equal proportions of seedlings from each seed size class in each site. Each seedling was tagged (keeping the number originally assigned to the seed), and its initial size and location recorded.

Starting in September 1991, censuses were taken in which seedling survival and growth (shoot height, basal diameter, and crown area) were recorded monthly until September 1992 and every two months thereafter until the end of March 1993. Seedling damage was recorded as partial

height loss (due to herbivory or top dieback) or total aboveground loss (due to desiccation, herbivory, or some other cause as rotting). Subsequent censuses revealed whether the loss was temporary (i.e. the seedling resprouted) or not.

Since the forest border is a more heterogeneous habitat, an attempt was made to classify the habitat of each seedling in order to compare survivorship among them. Each seedling's microsite was classified as: a) shaded, usually under the crown of established trees or large shrubs, b) partially shaded, covered by shrubs or close to the edge of the crown of established trees, or c) open.

Data analysis

Data on seed removal were analysed by comparing survival of each seed cluster (i.e., number of days elapsed until the last seed of the cluster disappeared) among sites with a logrank test, a non parametric test for comparing two or more samples (Pyke and Thompson 1986, Hutchings et al. 1991). Although the survival curves were constructed considering the total observation period of two months, the statistical comparisons were made on data at 35 days, taking into account that seeds placed on favourable conditions germinate soon after falling to the ground, and those under unfavourable conditions do not remain viable after this period.

Differences among sites in the proportions of seeds germinated and seedlings established per seed were tested using ANOVA. Data were arcsine transformed. Seedling survival was analysed using a proportional hazards statistical model, a semiparametric test that analyses the effect that a set of variables has in the "failure time" (in this case time until death) of an individual. The proportional hazards model allows comparisons of the distributions of lengths of failure times for each treatment or set of circumstances including censored individuals (in this instance those still alive at the end of the study period). The proportional hazards model is:

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$$\lambda \, (t;Z) = \lambda_0 \, (t) \, \exp \, \{ \beta_1 Z_1 + \beta_2 Z_2 + \ldots \beta_n Z_n \}$$

where t is the time since the start of the observation, $\lambda_0 \, (t)$ is an unspecified base-line hazard, and **Z** is a vector of binary variables that defines the treatments. It is assumed that the e^z have multiplicative effects with relative weights of β_i ($i = 1, 2, \ldots n$). This assumption assures that the resulting hazard rate, $\lambda \, (t;Z)$, is positive for all possible values of the Z_i s and the β_i s, and implies that when the value of Z_k is changed from A to B, the hazard rate is multiplied by a factor $\exp \, (\beta_k \, (A-B))$. Thus, the meaning of the coefficients β_i is straightforward and allows simple tests of the relative influence of the treatments Z_i ($i = 1, 2 \ldots n$), by comparing their relative risk e^β (Haccou and Hemerik 1985, Muenchow 1986). A test for the effect of Z_i is carried out by testing the null hypothesis $\beta_i = 0$ using a normal statistic value. The analysis was made using the S-PLUS language.

Data on proportions of seedlings resprouting during the period growth was recorded were analysed by means of logit analysis for binomial data (i.e., proportions, Crawley 1993), using the GLIM 3.77 statistical package. Differences among sites in seedling growth were analysed by comparing heights, diameters and crown areas of seedlings at the beginning and end of each growing season by means of a Kruskal-Wallis test. Within each site, a chi-square test was performed in order to test if there were differences in the proportions of surviving seedlings originated from small, medium and large seeds.

Results

Site characterization

The differences in canopy cover between sites were associated with differences in other physical characteristics. For instance, deep soils predominate at the closed forest site, while the disturbed site is dominated by a rocky substrate, with a low proportion of microsites having soil and litter (Fig. 1). The open oak canopy of the border area is established on a more heterogeneous (patchy) substrate that can be considered as a transition between the former two sites. Throughout the year, maximum air temperatures were consistently 10-13 °C higher at the disturbed site than at the forest interior (Fig. 2). Photosyntethically active radiation (PAR) reaching the soil is 1000-1300 μmol m^{-2} s^{-1} between 9:00 and 15:00 at the disturbed site, while at the forest floor it is 5-8% of that at the disturbed site from 12:00 to15:00 and less than 5% the rest of the time. At the forest border seedlings face a wide variety of light regimes, but mean PAR values are 10-22% of those found in open conditions between 10:00 and 17:00.

The pattern of rainfall is markedly seasonal and the length of the growing season is determined by the availability of water. Data of the nearest weather station showed that the first growing season ended in October 1991, the second growing season lasted from May to November 1992, and the initiation of the third growing season was delayed until June, because of unusually low rainfall during May 1993 .

Seed predation and seedling establishment

Acorns on the ground face a high risk of predation by small mammals, particularly ground squirrels (*Spermophilus variegatus*) and mice (*Peromyscus gratus*). All acorns in the high density clusters were gone after two months regardless of the site, while 30 % of them remained in the five and one-seed clusters at the forest interior and in the one-seed clusters at the disturbed zone (Fig.

3). Regardless of density, all seeds at the forest border had disappeared after two months. In all cases, however, some seeds remained on the ground for 35 days, which is enough time for a seed to germinate and produce a seedling. After 35 days the highest rate of removal corresponded to the 25-seed clusters at the forest border, where 2% of the seeds remained on the ground, while varying proportions, ranging from 10% to 70% of the seeds survived in other cases (Fig. 3). There were significant differences among sites for the 5 and 25 seed densities (Table 1), with more seeds than expected removed both at the forest border and at the forest interior and equal or fewer seeds removed at the disturbed site.

Seed germination and establishment (i.e. seedling rooting and elongation of the first flush of leaves) differed among sites ($P<0.001$ and $P<0.001$, respectively; Table 2), with significantly lower values in the disturbed zone, but no differences between the forest interior and the forest border. All seeds located in completely open microsites were dry in less than a week and only those under some kind of protective shade were able to germinate. The main causes of germination failure at the forest interior and the forest border were acorn rotting due to fungal attack and predation of the emerging radicle (possibly by diptera larvae).

Seedling survival and growth

More than 95% of the seedlings at the forest border and at the disturbed site survived the first rainy season (Fig. 4). At the forest interior mortality was slightly higher (12%), mostly due to the action of rabbits and small rodents that severed the shoots. The first dry season (Nov. 91- Apr. 92) had a great impact on survival at the disturbed site, where approximately 60% of the seedlings died. The most conspicuous decline occurred in February and March, during a period of about 50 days without any appreciable precipitation (personal observation). Seedlings at the forest border and the forest interior showed a higher survival, with only 13% and 19% of them dying during this dry season, respectively .

During the second growing (rainy) season (May-Nov. 1992) no seedlings died at the disturbed site and mortality was also very low at the forest border. As in the first growing season, more seedlings died at the forest interior during this period, mainly due to herbivory and fungal attack. At the end of the two growing seasons the disturbed site had the lowest overall seedling survival (35%), followed by the forest interior (60%), and the forest border (76.5%, Fig. 4). The second dry season had a great impact on seedling survival, causing a drop from 76% survival to 52% at the forest border, similar to the final survival at the forest interior. Only 5% of the seedlings at the disturbed site were alive after this drought period.

In the two proportional risk analyses made (one at the end of the second growing season and the other at the beginning of the third growing season), the forest interior was taken as the baseline against which comparisons were made (i.e., the baseline risk obtained when the z_i were zero). In both cases the model was highly significant, as judged by the likelihood ratio test (Table 3). At the end of the second growing season (Nov. 92) there were significant differences among the three sites, with the seedlings at the forest border having a 50% lower relative risk compared to the ones found at the forest interior, while at the disturbed site the risk was 80% higher than at the forest interior. By April 93, risk at the forest border had increased and was no longer significantly different from the forest interior, while at the disturbed site the difference increased, with a final risk 150% larger than that at the forest interior.

The effect of the harsh second dry season (December 92 - May 93) is also evident in a comparison of seedling survival in each of the three types of microsites registered within the forest border (Fig. 5). At the end of the second growing season (Nov. 92) there was relatively high survival irrespective of the microsite, but at the end of March 1993 differences between partially shaded and open microsites had increased greatly.

The relative importance of the different agents of mortality varied among sites (Table 4). Overall, desiccation during the dry season was the main cause of seedling death at the disturbed site, while herbivory and rotting were particularly important at the forest interior, the main herbivore

being the rabbit *Sylvilagus floridanus*. At the forest border there was not a single outstanding cause of death until the end of the second growing season, but after the 1993 dry season desiccation increased in importance, accounting for 62% of the mortality observed.

Out of a total of 204 dead shoots, 40% resprouted. There were not significant differences in the proportion of seedlings resprouting at the disturbed site (32%), the forest border (41%), and the forest interior (49%). The cause of shoot death significantly affected resprouting (P =0.001), with a higher probability of resprouting after herbivory (59%) than when a shoot desiccated (23%) or rotted (29%).

At all three sites, there was a higher probability of resprouting if damage occurred during the rainy season (63%) than during the dry season (28%). At the disturbed site it is difficult to separate the effects of timing (i.e., shoot death occurring during the dry or de rainy season) from desiccation, which leads to a low resprouting capacity. At the forest interior, where most damage to the seedlings was produced by herbivory, this seasonal pattern persisted (64% vs. 31% resprouting after damage in the rainy and dry seasons, respectively). The period between damage and emergence of a new shoot varied between one and six months, with the great majority of resprouting events occurring during the first three months. Late resprouting was more common at the forest interior than at the other two sites.

In addition to the cases where all or most of the shoot died, there were frequent cases of partial dieback and partial removal by herbivores. Overall, 70% of the seedlings experienced some kind of aboveground biomass loss during both growing seasons. Most of the partial losses were followed by new growth.

There was not an overall significant relationship between seed size and seedling survival (X^2 = 2.88 d. f. 2 P = 0.23). Only at the forest border were significant differences observed, with seedlings from large seeds displaying a higher survival. At the end of the second dry season

(March 93) there were significant differences at the forest border in the proportion of survivors coming from different seed sizes ($P<0.01$) , and a further census (August 1993) showed that they increased during the third growing season with 70, 44 and 19% of surviving seedlings originating from large, medium and small seeds, respectively (Fig. 6).

As with survival, there were differences in seedling growth among sites. At the forest interior seedlings were shorter and had lower diameters and crown areas throughout both growing seasons (Table 5), while at the disturbed site seedlings had higher growth rates but were severely affected by drought. During the first dry season, mean seedling size declined noticeably at this site, although there was a gradual recovery in height and a greater recovery in crown area of surviving seedlings during the second rainy season (Figs. 7 and 8). Some seedlings resumed growth better than others and, as a consequence, the variance in seedling size increased with time. At the forest border seedlings had a more moderate height growth, and although there was a loss of foliage during the first dry season, it was followed by a rapid recovery with the onset of rain. The harsher second dry season caused an abrupt decline in crown area, similar to the one seedlings experienced at the disturbed site (Fig. 8). However, the maintenance of a living shoot with a diameter that had increased continuously during the previous growing seasons (Table 5) allowed a rapid recovery of foliage in the next growing season (data not shown).

Shoot heights of seedlings that did not suffer any kind of aerial biomass loss until the end of the second growing season were similar between seedlings at the disturbed site and at the forest border (mean = 18.1 cm in both cases) and higher than shoot height of seedlings at the forest interior (13.7 cm). At the end of the second growing season mean crown area of these intact seedlings had increased 200% at the disturbed site, 145% at the forest border, and 50% at the forest interior (mean values 156.2, 130.3 and 60.6 cm^2 at each site, respectively). These data show that intact seedlings attained larger mean sizes than the overall population at each site (Table 5) and that the frequent loss of aerial biomass reduced seedling growth.

Discussion

High post-dispersal acorn predation is common (Shaw 1968, Griffin 1971, Crow 1988, Quintana Ascencio et al. 1992, Barik et al. 1996) and can limit oak regeneration. The rapid disappearance of high density seed clusters, probably due to an increased conspicuousness of clumped seeds, has been previously documented (Price and Jenkins 1986). The higher removal rates at the forest border and forest interior may reflect preferential foraging by small mammals, which are the main predators at the site, and the delayed consumption found at the disturbed site may be attributable to lower mammal densities and/or lower searching activities, as there has not been acorn production at this site since the disturbance in 1989.

Most of the removed acorns were eaten, as judged by the frequent leftover shells. However, some removed acorns may be buried in caches by small mammals (Barnet 1977) or birds (Bosema 1979, Darley Hill and Johnson 1989) and might escape predation if they germinate and become established seedlings before being recovered by a predator (Jensen and Nielsen 1986, Crow 1988). In our study, this may occur at the forest interior and parts of the forest border, but not at the disturbed site, due to the impossibility of digging in the rocky substrate.

A proportion of seeds, most from the low density clusters, remained in the ground long enough to germinate under adequate conditions. These conditions may be met in those years with frequent rains during the period from November to January, simultaneous with or soon after seed shedding. Laboratory test have shown that under favourable conditions 85% of viable *Quercus rugosa* acorns germinate after five weeks, with a Gt_{50} of 15 days (Robledo 1997). It is very unlikely that there is a significant amount of germination and establishment later than January, given that acorns usually do not remain viable in the soil for long periods of time and would have to escape predation and remain viable on the ground 4-5 months, until the onset of the rainy season in May.

Once a sound acorn has escaped predation, the germination and establishment probabilities are relatively high at the forest border and the forest interior (Table 2). The lower values found at the disturbed site are probably related to the high temperatures near the ground and the relative scarcity of shaded microsites that protect the seeds and seedlings from desiccation. Additionally, the nature of the substrate at this site (basaltic rock) makes radicle penetration possible only in crevices where soil has been deposited. It has been reported at other localities that hard soils and high temperatures prevent oak regeneration (Griffin 1971) and acorns exposed to full, day-long sunlight have little chance of germination (Lathrop and Osborne 1990, Nyandiga and McPherson 1992).

The above has implications for the reintroduction of oaks at this site. It seems that planting acorns is not a sound restoration technique, as substrate characteristics prevent high-density sowing and deep burial of acorns and thus favour both acorn desiccation and predation. Other restoration techniques, based on seedling and juvenile introduction may prove more successful, as discussed below.

Seedling survival differed strongly by site. The high death rates found at the disturbed site during both dry seasons strongly suggest that low water availability, especially during the period from December to April, is the main factor limiting seedling survival. In the absence of frequent rain, the high temperatures near the ground and the porous rocky substrate that does not retain moisture cause extensive seedling death. The low death rates registered during the rainy season at this site in both years reinforce this view, as high temperatures continue until July (Fig.2) without causing seedling death once there is enough precipitation. Dehydration has also been reported as the most important death cause of *Quercus engelmanii* seedlings in California's mediterranean climate (Lathrop and Osborne 1990) and Barik et al. (1996) have reported low oak seedling mortality in Indian locations with high moisture availability.

The higher survival of seedlings planted in the forest border until the end of the second growing season is likely related to the presence of a semi-open canopy that protects the seedlings

from solar radiation and desiccation (Quintana-Ascencio et al. 1992, Thadani and Ashton 1995). Comparison between the two years suggest that, as a whole, this environment can maintain relatively high seedling survival when the drought is not too severe. When drought is more pervasive the importance of the specific microsite occupied by the seedling increases (Fig. 5) and persistence is closely associated with relative position under the canopy of established trees or shrubs. Muick (1991) and Callaway (1992) also fond that shade and shrubs exert a facilitative effect on *Q. douglasii* seedlings. This facilitation process is frequent in those habitats, like deserts and sand dunes, where seedlings are likely to experience water deficiency (Turner et al 1969, Valiente-Banuet and Ezcurra 1991, Kellman and Kading 1992). At the forest interior the canopy and the litter favor the maintenance of soil humidity throughout most of the year and, in those conditions, herbivory and rotting, which are common in seedlings growing under closed canopies (Augspurger 1984, Takenaka 1986, Khan and Thripathi 1991) increase in importance.

Resprouting made an important contribution to seedling survival. The proportion of seedlings resprouting was high, though similar to the 35% reported for *Q. engelmanii* in California (Lathrop and Osborne 1990). The lack of a significant association between ability to resprout and site could be influenced by the fact that all seedlings had been grown in the nursery for approximately four months before being planted, and therefore had probably accumulated similar levels of photosyntates. *Quercus leucotrichopora* seedlings growing beneath a closed canopy are less likely to possess enough carbohydrates to resprout (Thadani and Ashton, 1995). While biomass removal by herbivores does not imply any harm to the root, shoot desiccation probably entails root desiccation and thus seedling death. This is likely to account for the relationship observed between resprouting and cause of shoot loss. Resprouting capacity and water availability were also correlated, as shown by the differences found between the dry and rainy seasons. A significant correlation between timing of aerial biomass reduction and seedling survival and growth has been described in other tree species (Canham et al. 1994).

A relationship between seed size and survival was evident only under the relatively favorable conditions of the forest border. Other studies have shown a significant correlation between seed mass and oak seedling survival in the field (Tripathi and Khan 1990) and under experimental reduction of biomass (Aizen 1996, Bonfil 1998), although it is not clear whether it is a general phenomenon in the genus (Long and Jones 1996). Our results point to the conclusion that under conditions favourable for seedling survival, differences established early during seedling development increase with time.

As with survival, seedling growth was limited by moisture deficiency where open conditions prevailed, as shown by the abrupt declines in seedling size during each dry season at the disturbed site. Although surviving seedlings were able to recover at varying rates, the numbers surviving after two periods of drought were too low to make a contribution to a substantial recovery of the population. At the forest border the decline in size was less pronounced and a lower proportion of seedlings experienced size reductions.

The low seedling growth found at the forest interior confirms the view that the shaded conditions of a closed canopy are inappropriate for oak seedling growth (Takenaka 1986, Crow 1992, Quintana-Ascencio et al 1992). Significant reductions in the growth of other oak seedlings have been observed when grown in 8%-10% of full sunlight (Phares 1971, Gottschalk 1985). The behaviour of planted seedlings of Q. rugosa under the forest canopy suggests that this is not a shade-tolerant species and the lack of persistence of naturally established seedlings under the forest canopy supports this assertion.

Undamaged seedlings at both the forest border and the disturbed site showed no differences in height, but the larger crown area of intact seedlings growing at the disturbed site and data on basal diameter (which is related to root biomass) suggest that they probably had larger total dry mass at the end of the second growing season, as has been described in other oak seedlings growing in full sunlight (Ovington and MacRae 1960, Phares 1971, Gottschalk 1985, Crow 1992). Overall, growth was not severely reduced under the semi-open canopy of the forest border (Table 5)

and the significantly higher proportion of seedlings growing and surviving at this site indicate that these conditions promote oak regeneration.

These results show that extensive reintroduction of *Quercus rugosa* to the disturbed site will probably fail under present conditions. Neither seed sowing nor high density seedling input seem to be good techniques for improving regeneration in this case. An alternative and ecologically more sound method should include selection of suitable microsites along the border of the forest or the selection or duplication of environmental conditions that mimic the forest border. The partial shade provided by trees or shrubs seems to be especially relevant and established trees of *Buddleia cordata* and other large shrubs could be used; they are also a source of litter that may help to ameliorate fluctuations in soil temperatures. Substrate conditions could also be improved by deep planting and soil addition while planting. Selection of large seeds is advisable if one-year old seedlings are to be used. In view of the importance of resprouting for survival, it is desirable to grow seedlings in relatively large containers and particular care of the seedling roots is required during transplanting, as starch reserves used for resprouting are stored in the roots.

Much of the common practice of reforestation programs in Mexico relies on large-scale production of seedlings that are then transplanted extensively without a proper selection of adequate species, planting sites, and seedling quality (Mexal 1997). Our work points to a different strategy which might be generalised to similar sites. This requires better trained personnel, more effort per plant and a lower overall density of seedlings planted. Under present conditions, such a method would likely yield a higher success in restoration programs.

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References

Aizen M. A. and H. Woodcock. 1996. Effects of acorn size on seedling survival and growth in *Quercus rubra* following simulated spring freeze. *Can. J. Bot.* 74: 308-314

Alvarez Cruz E. M. 1992. *Condiciones de temperatura y precipitación en el SW del Distrito Federal.* Thesis. Colegio de Geografía, Facultad de Filosofía, UNAM, México.

Aragón F. 1993. *Evolución de los procesos socioambientales del Ajusco Medio. Estudio de la dinámica de la Reserva Ecológica del Ajusco y su interrelación con las zonas contiguas.* Thesis. Master in Urban Development. El Colegio de México.

Augspurger C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps and pathogens. *Ecology* 65: 1705-1712.

Barik S. K., P. Rao, R. S. Tripathi and H. N. Pandey. 1996. Dynamics of tree seedling populations in a humid subtropical forest of northeast India as related to disturbance. *Can. J. For. Res.* 26: 584-589.

Barnett R. J. 1977. The effect of burial by squirrels on germination and survival of oak and hickory nuts. *Am. Midl. Nat.* 98: 319-330.

Bonfil C. 1998. The effects of seed size, cotyledon reserves and herbivory on seedling survival and growth in *Quercus rugosa* and *Quercus laurina* (Fagaceae). *Am. J..Bot.* 85: 79-87 (in press)

Bonfil C., I. Pisanty, A. Mendoza and J. Soberón. 1997. Investigación y restauración ecológica: el caso del Ajusco Medio. *Ciencia y Desarrollo* 135:15-23.

Bonner F. T. and J. A. Vozzo. 1987. *Seed biology and technology of* Quercus. Gen. Tech. Rep. SO-66. New Orleans, LA: US Dept. of Agric., Forest Service, Southern Forest Experiment Station. 21 p.

Bossema I. 1979. Jays and oaks: an eco-ethological study of symbiosis. *Behaviour* 70: 1-117

Callaway R. M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73: 2118-2128

Canham C.D., J. B. McAninch and D. M. Wood. 1994. Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. *Can. J. For. Res.* 24: 817-825

Carvell K. L. and E. H. Tryon. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. *For. Sci.* 7:98-105.

Cordova C., A. L. Martín del Pozo and J. López Camacho. 1994. Paleolandforms and volcanic impact on the environment of prehistoric Cuicuilco, southern Mexico City. *J. Arch. Sci.* 21: 585-596

Crawley M. J. 1993. *GLIM for Ecologists.* Blackwell Scientific Publications, London.

Crow T. R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)- A review. *For. Sci.* 34:19-40

Crow T.R. 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. *Oecologia* 91:192-200

Darley-Hill S. and W. C. Johnson. 1981. Acorn dispersal by the Blue Jay (*Cyanocitta cristata*). *Oecologia* 50:231-232

Ezcurra E. 1990. *De las chinampas a la megalópolis: el medio ambiente en la cuenca de México.* Fondo de Cultura Económica Col. La Ciencia desde México. México, D.F.

Gottschalk K. W. 1985. Effects of shading on growth and development of northern red oak, black oak, black cherry and red maple seedlings. I. Height, diameter and root/shoot ratio. Proceedings of the Fifth Central Hardwood Forest Conference. Soc. of American Foresters, Washington, D.C. pp 189-195

Griffin J. R. 1971. Oak regeneration in the upper Carmel Valley, California. *Ecology* 52:862-868

Grime. J. P. and D.W. Jeffrey. 1965. Seedling establishment in vertical gradients of sunlight. *J. Ecol.* 53:621-642

Grubb P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52:107-145.

Haccou P. and L. Hemerik. 1985. The influence of larval dispersal in the cinnabar moth (*Tyria jacobea*) on predation by the red wood ant (*Formica polyctena*): an analysis based on the proportional hazards model. *J. Anim. Ecol.* 54: 755-769.

Harper J. 1977. *Population Biology of Plants.* Academic Press, New York.

Hutchings M., K.. D. Boothand S. Waite. 1991. Comparison of survivorship by the longrank test: criticisms and alternatives. *Ecology* 72:2290-2293

Jensen T. S. and O. F. Nielsen. 1986. Rodents as seed dispersers in a heath-oak wood succesion. *Oecologia* 70:214-221.

Kellman M. and M. Kading. 1992. Facilitation of tree seedling establishment in a sand dune succession. *J. Veg. Sci.* 3:679-688

Khan M. L. and R. S. Tripathi. 1991. Seedling survival and growth of early and late succesional species as affected by insect herbivory and pathogen attack in sub-tropical humid forest stands of north east India. *Acta Oecol.* 12: 569-579

Lathrop E. W and C. Osborne. 1990. From acorn to tree: ecology of the engelmann oak. *Freemontia* 18: 30-35

Long T. J. and R. H. Jones. 1996. Seedling growth strategies and seed size effects in fourteen oak species native to different soil moisture habitats. *Trees* 11: 1-8

Matzuda K. and J. R. McBride. 1986. Difference in seedling growth morphology as a factor in the distribution of three oaks in central California. *Madroño* 33: 207-216

McComb A. L. 1934. The relation between acorn weight and the development of one year chestnut oak seedlings. *J. For.* 32:479-484

Mexal J. G. 1997. Forest nursery activities in Mexico. *National Proceedings: Forest and Conservation Nursery Associations 1996.* USDA Forest Service Gen. Tech. Rep. PNW-GTR-389: 228-232

Muenchow G. 1986. Ecological use of failure time analysis. *Ecology* 67:246-250

Muick P. C. 1991. Effects of shade on blue oak and coast live oak regeneration in California annual grasslands. USDA For. Serv. Gen. Tech. Rep. PSW-126:21-24

Nixon K. C. 1990. The genus *Quercus* in Mexico. In: Ramamoerthy T.P., R. Bye and J.E. Fa (eds.). *Biological Diversity of Mexico*. pp. 447-458. Oxford University Press:

Nyandiga C. O. and G. R. McPherson. 1992. Germination of two warm-temperate oaks, *Quercus emoryi* and *Quercus arizonica. Can. J. For. Res.* 22: 1395-1401

Ovington J. D. and C. MacRae. 1960. The growth of seedlings of *Quercus petrae. J. Ecol.* 48: 549-555

Phares R. E. 1971. Growth of red oak (*Quercus rubra* L) seedlings in relation to light and nutrients. *Ecology* 52:669-672.

Price M. V. and S. H. Jenkins. 1986. Rodents as seed consumers and dispersers. In: D. R. Murray (ed.). *Seed dispersal*. pp: 191-235. Academic Press, New York.

Pyke D. A. and J. N. Thompson. 1986. Statistical analysis of survival and removal rate experiments. *Ecology* 67: 240-245

Quintana Ascencio P., M. G. Espinoza and N. Ramírez Marcial. 1992. Acorn removal, seedling survivorship, and seedling growth of *Quercus crispipilis* in succesional forests of the highlands of Chiapas, México. *Bull..Torr.Bot. Club* 119: 6-18.

Robledo A. 1997. *Germinación y crecimiento de plántulas de cuatro especies de encinos del Ajusco D.F. Efecto del tamaño de semilla*. Thesis. Facultad de Estudios Superiores Zaragoza. Universidad Nacional Autónoma de México. México D.F.

Rzedowski, J. 1981. *Vegetación de México*. Ed. Limusa, México.

Shaw M. W. 1968. Factors affecting the natural regeneration of sessile oak (*Quercus petraea*) in North Wales. II. Acorn losses and germination under field conditions. *J. Ecol.* 56: 647-660.

Takenaka A. 1986. Comparative ecophysiology of two representative *Quercus* species appearing in different stages of succesion. *Ecol. Res.* 1:129-140.

Thadani R. and P. M. S. Ashton. 1995. Regeneration of banj oak (*Quercus leucotrichopora* A. Camus) in the central Himalaya. *For. Ecol. Manag.* 78: 217-224

Tripathi, R. S., and M. L. Kahn. 1990. Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of *Quercus* in a subtropical wet forest. *Oikos* 57: 289-296.

Turner, R. M., S. M. Alcorn and G. Olin. 1969. Mortality of transplanted saguaro seedlings. *Ecology* 50: 835-844.

Valiente-Banuet A. y E. Ezcurra. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, México. *J. Ecol.* 79:961-971.

Welker J. M. and J. W. Menke. 1990. The influence of simulated browsing on tissue water relations, growth and survival of *Quercus douglasii* (Hook & Arn) seedlings under slow and rapid rates of soil drought. *Funct. Ecol.* 4:807-817

Zavala F. 1990. Los encinos mexicanos: un recurso desaprovechado. *Ciencia y Desarrollo* 95: 43-51

Table 1. Logrank test for comparisons of seed removal between sites for each seed density.

Density	site	d_i	E_i	LR	d.f.	P
1	D	6	6.54			
	B	9	4.82			
	F	6	8.64	4.47	2	0.10
5	D	15	33.9			
	B	41	28.3			
	F	35	28.8	17.57	2	<0.001
25	D	205	278.9			
	B	246	215.1			
	F	225	182.0	34.20	2	<0.001

d_i = number of seeds removed per site (D = disturbed, B = forest border, F = forest interior)

E_i = total expected numbers of seeds removed

$$LR = \frac{(d_1 - E_1)^2}{E_1} + \frac{(d_2 - E_2)^2}{E_2} + \frac{(d_3 - E_3)^2}{E_3}$$

Table 2. Acorn germination and seedling establishment (mean ± s.d.)

Site	GERMINATION		ESTABLISHMENT	
	%	s. d.	%	s. d.
Disturbed	46.81 [a]	40.01	0.92 [a]	3.2
Forest Border	73.02 [b]	22.5	20.63 [b]	15.6
Forest Interior	92.22 [b]	10.4	15.45 [b]	15.7

* different letters in the same column indicate significant differences between sites, according to Tukey's HSD test ($P < 0.05$)

Table 3. Proportional risk analysis of the effect of site on seedling survival

November 1992

Variable	β	std. error	relative risk (e^{β})	(e^{β}) lower .95	(e^{β}) upper .95	z-values	P
Disturbed	0.583	0.20	1.79	1.20	2.68	2.84	0.004
F. Border	-0.694	0.26	0.50	0.30	0.84	-2.63	0.008

Likelihood ratio test 31.9 d.f. 2 $P = 0.001$

April 1993

Variable	β	std. error	relative risk (e^{β})	(e^{β}) lower .95	(e^{β}) upper .95	z-values	P
Disturbed	0.918	0.18	2.50	1.75	3.55	5.07	0.004
F. Border	-0.216	0.21	0.81	0.54	1.21	1.04	n. s.

Likelihood ratio test 47.8 d.f. 2 $P < 0.0001$

Table 4. Total seedling mortality and percentage mortality by causes (July 91-Nov 92)

Site	N	causes of mortality (%)		
		desiccation	herbivory	others*
Disturbed	64	89.1	6.2	4.7
F. Border	23	30.4	39.1	30.4
F. Interior	38	7.9	60.5	31.6

* other causes include rotting, and in a few cases seedlings crushed by felled branches or uprooted.

Table 5. Shoot height, crown area and stem diameter of surviving seedlings at the end of the first growing season (Nov. 91), the first dry season (Apr. 92) and the second growing season (Nov. 92).

	HEIGHT (cm)			CROWN AREA (cm²)			DIAMETER (cm)		
	Nov 91	Apr 92	Nov 92	Nov 91	Apr 92	Nov 92	Nov 91	Apr 92	Nov 92
Disturbed	12.3 [a]	10.8 [a]	15.0 [a]	58.3 [a]	26.9 [a]	125.6 [a]	0.21 [a]	0.27 [a]	0.39 [a]
Border	11.7 [a]	13.1 [a]	15.4 [a]	49.4 [a,b]	51.9 [b]	88.9 [a]	0.20 [a]	0.24 [a]	0.28 [b]
F. interior	10.0 [b]	10.2 [b]	9.9 [b]	40.6 [b]	34.9 [a]	35.6 [b]	0.17 [b]	0.19 [b]	0.21 [c]

* different letters in the same column indicate significant differences between sites according to Tukey's HSD test ($p < 0.05$)
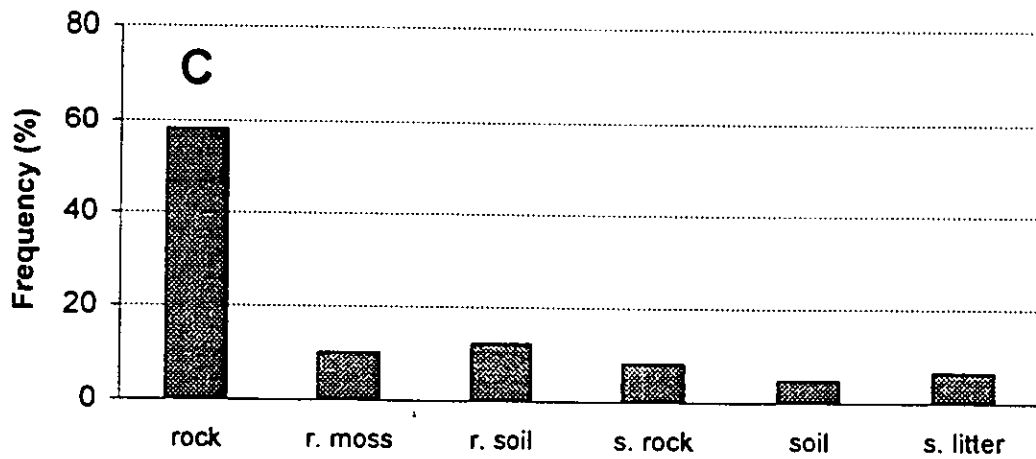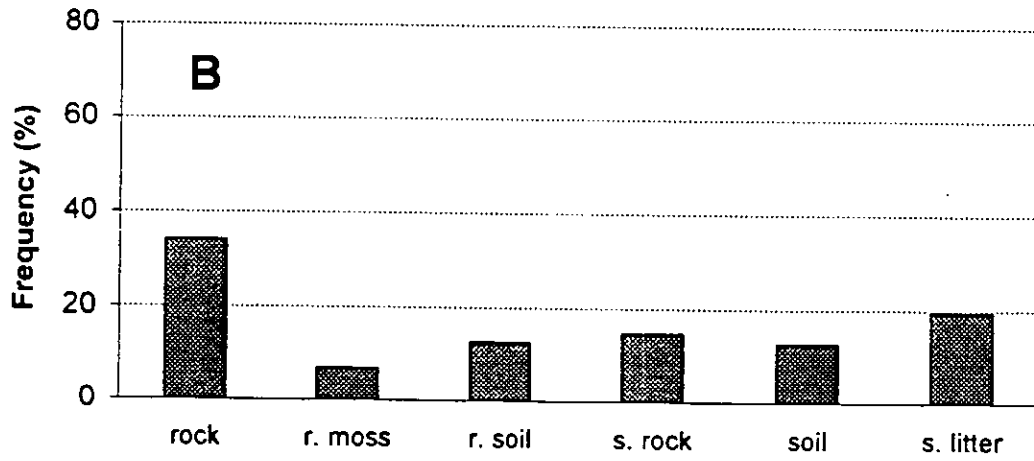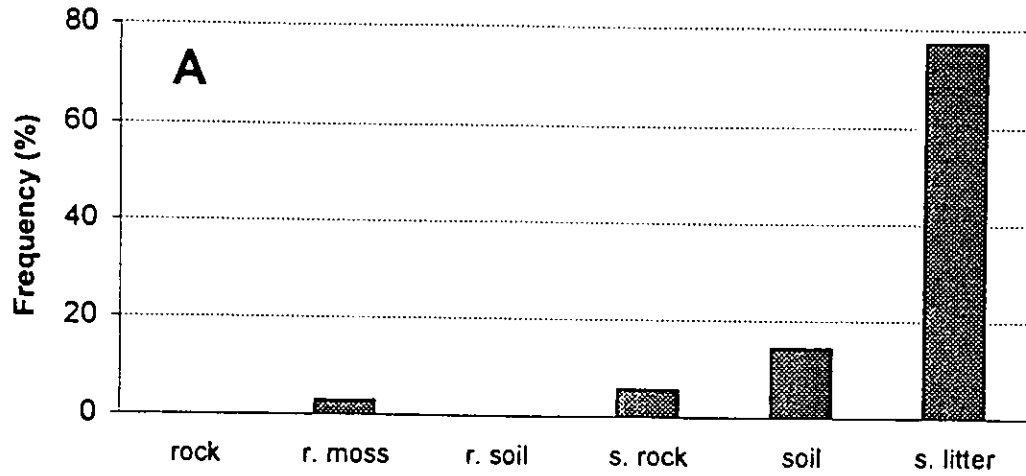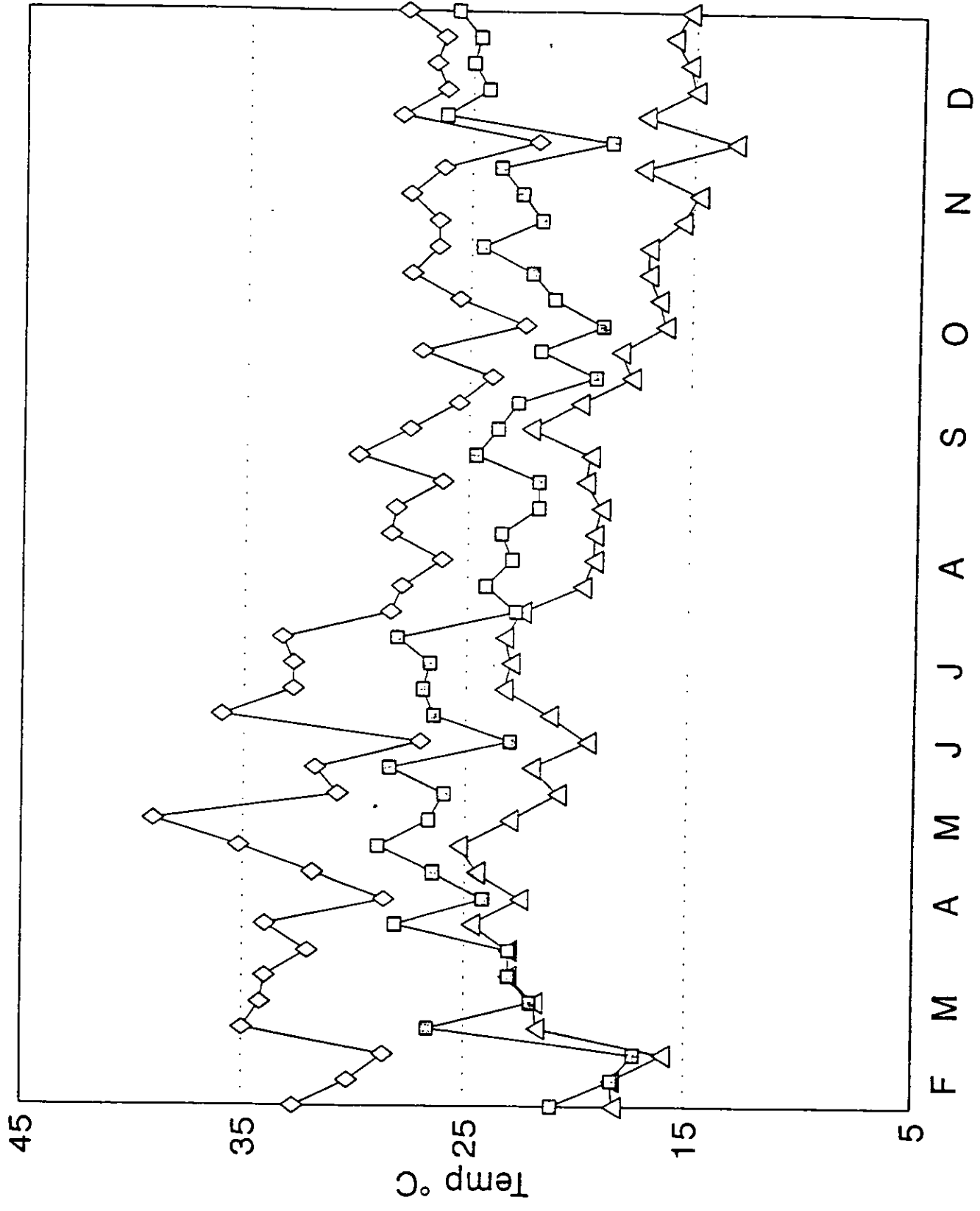
Figure 1

Figure 2
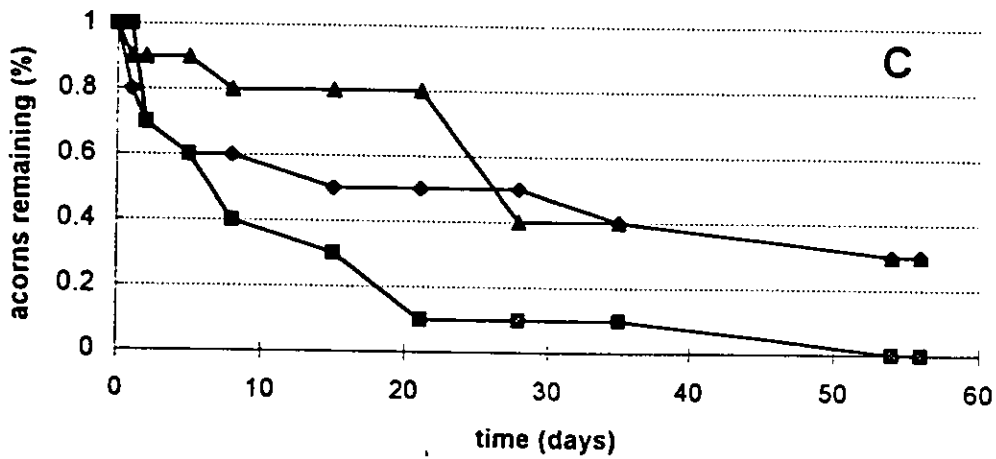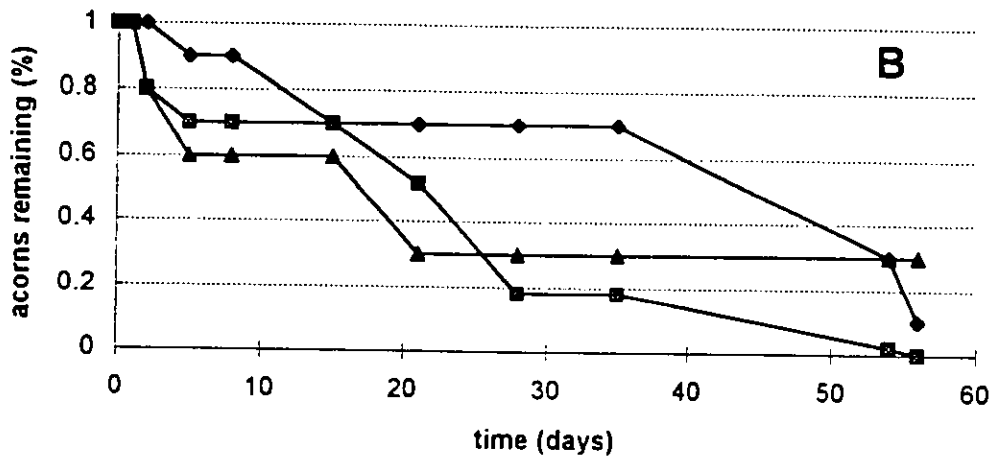
Figure 3

Figure 5

Figure 6

Figure 7
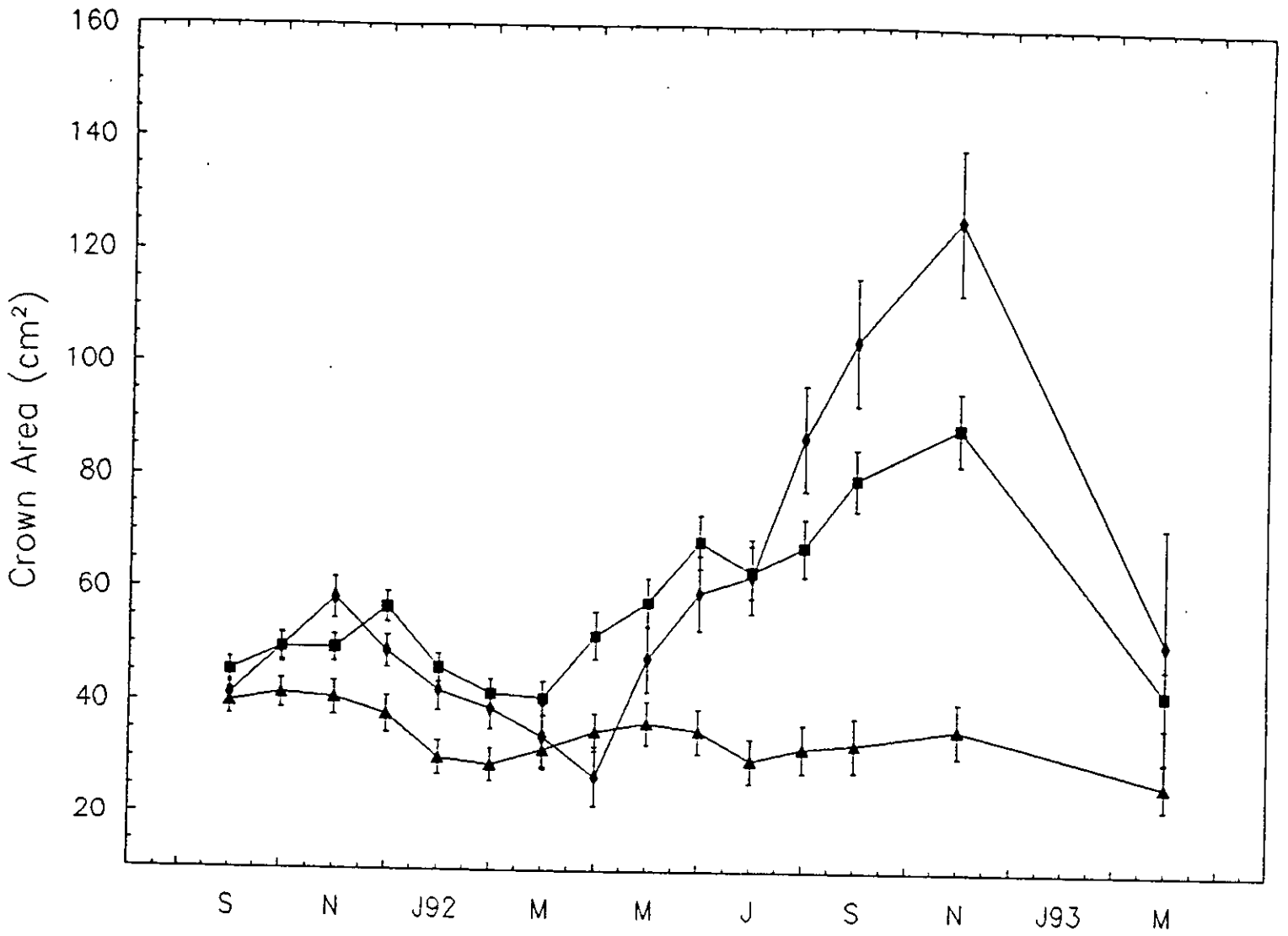
Figure 8

Figure Legends

Fig. 1. Superficial structure of the soil at: A) forest interior, B) forest border, and C) disturbed site. Categories: rock = bare volcanic rock, r. moss = volcanic rock with mosses or lichens, r. soil = volcanic rock with mosses or lichens and soil, s. rock = rock surrounded by soil, soil = soil without rocks, and s. litter = well developed soil covered by litter.

Fig. 2. Maximum temperature 30 cm above the ground at the disturbed site (♦), the forest border (■) and the forest interior (▲) during 1992.
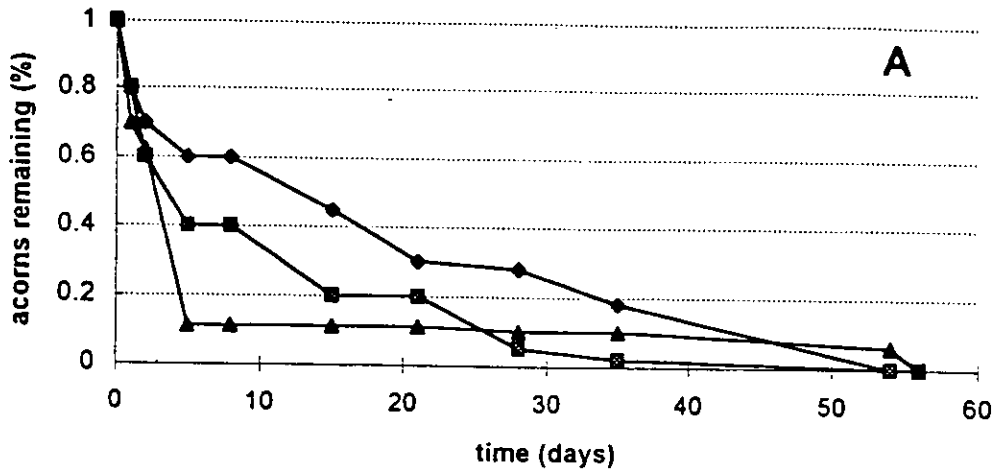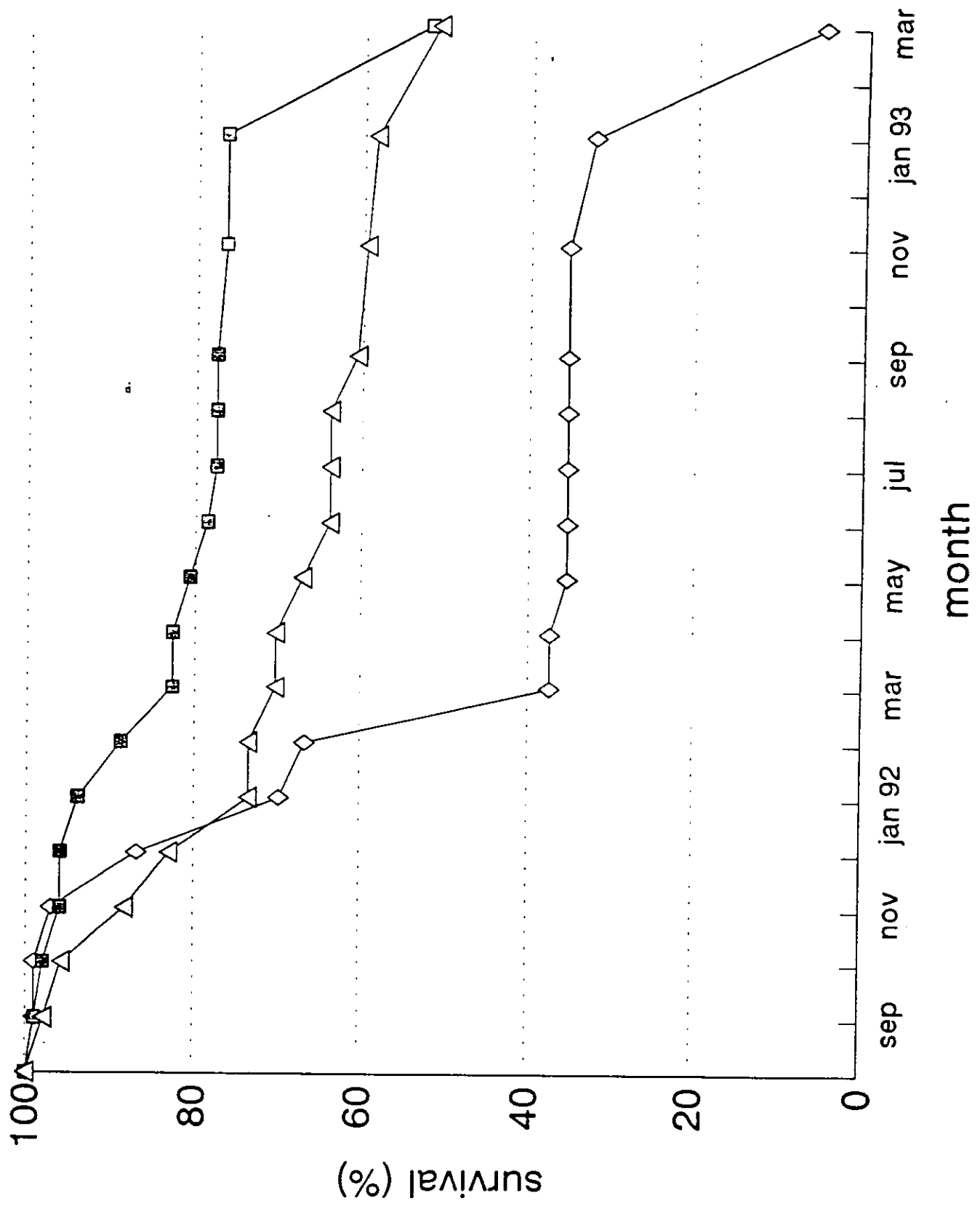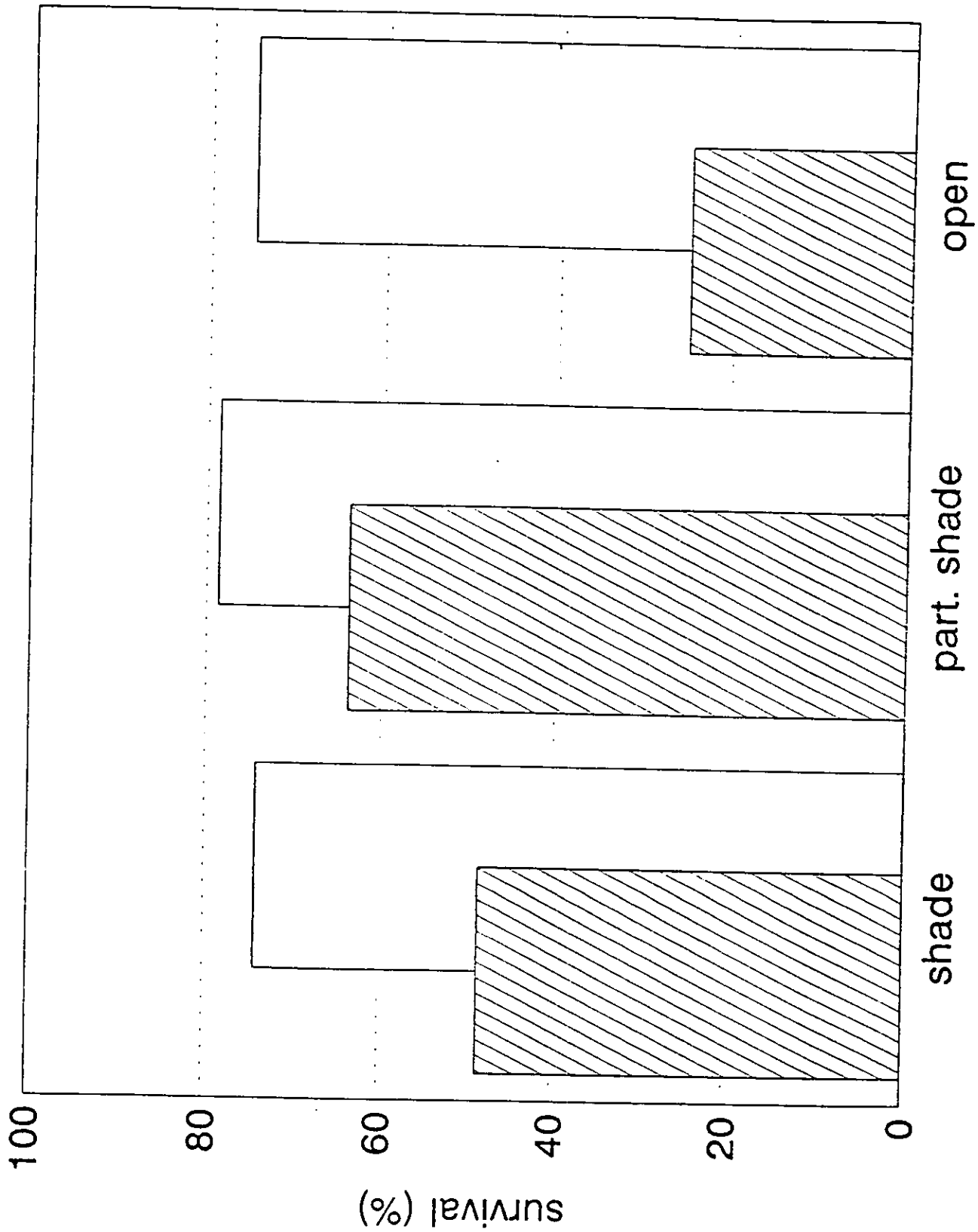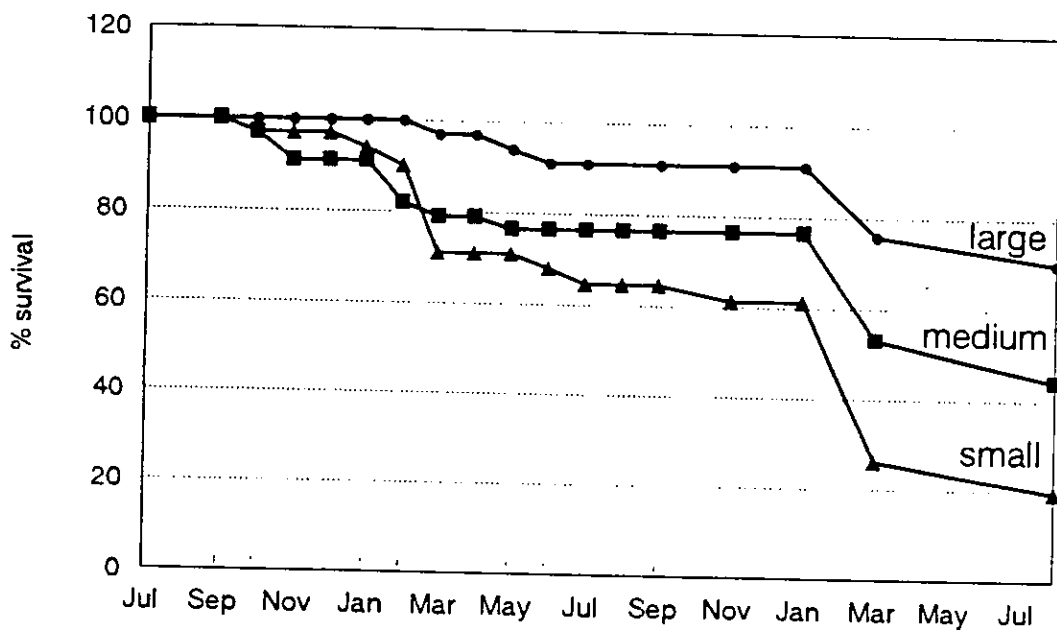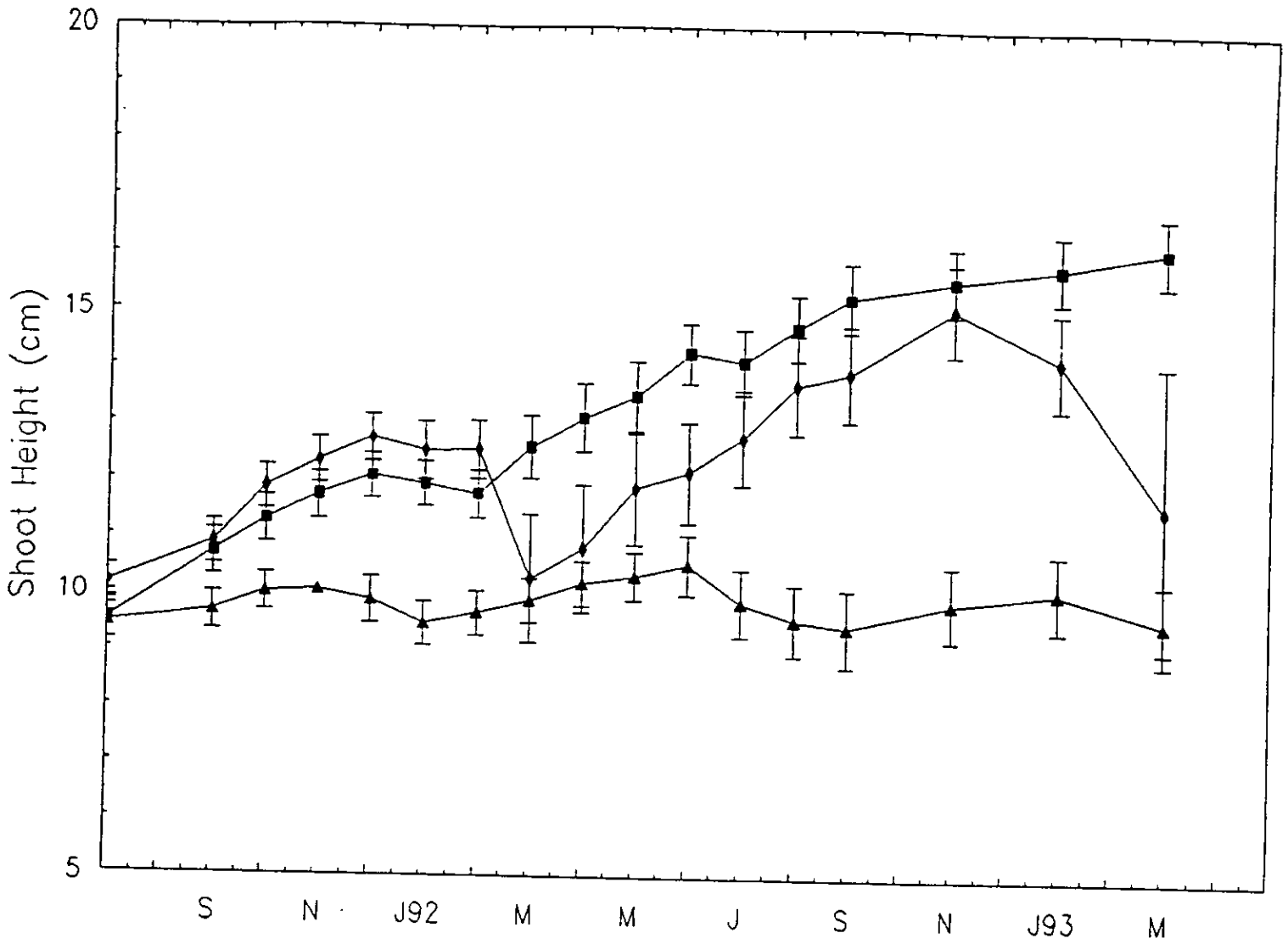
Fig. 3. Acorn removal rate at three seed densities. (A = 25 seeds, B = 5 seeds, and C = 1 seed) at the disturbed site (♦), the forest border (■), and the forest interior (▲).

Fig. 4. Seedling survival at the forest border (■), the forest interior (▲), and the disturbed site (♦) during September 1991-March 1993.

Fig. 5. Seedling survival at three microsites within the forest border in November 1992 (back) and March 1993 (front). N = 35, 47 and 16 for shaded, partially shaded and open microsites, respectively.

Fig. 6. Seedling survival from September 1991 to July 1993 at the forest border according to the size category of the seeds from which they originated.

Fig. 7. Height of *Quercus rugosa* seedlings at the forest border (■), disturbed site (♦) and forest interior (▲) from September 1991 to March 1993.

Fig. 8. Crown area of *Q. rugosa* seedlings at the disturbed site (♦), forest border (■) and forest interior (▲) from September 1991 to March 1993.

CAPÍTULO IV

Análisis demográfico de una población de encinos (*Quercus rugosa*) en la parte central de México: implicaciones para la restauración

Nicolas Moreno
1986

Demographic analysis of *Quercus rugosa* in central Mexico: implications for restoration

Introduction

Oaks and pines are the most important trees in the temperate forests of Mexico; they occupy large areas in all major mountain ranges. At present it is estimated that the extension of temperate broadleaf forests (in which oaks predominate) is around 9×10^6 ha, while coniferous forests occupy 17×10^6 ha (Masera et al. 1993). Mexico is also a center of diversification of *Quercus*. The number of species occurring in its territory has been estimated at 150, 85 of which are endemic (Nixon 1993). However, as many oak forests are found on areas particularly well suited for human settlement, they have been severely disturbed (Rzedowski 1981). Major disturbances are caused by expanding urban areas, forest fires, cattle grazing and logging. Additionally, oak wood is a major domestic fuel in rural areas, and during the first decades of the century was heavily exploited to produce charcoal. Its industrial use, although expanding, has been less common, due to poor knowledge of wood properties and the lack of adequate technologies.

As a result of these disturbances, many oak forests have disappeared or have been severely reduced and suffer from lack of regeneration, pest attack and loss of biodiversity. In view of the above it has become increasingly necessary to obtain information on the ecological behavior of a vast array of *Quercus* species, so that sound management and restoration programs can be designed.

Demographic studies may provide relevant information needed for these programs, as their primary goal is to understand the factors that determine population dynamics and its consequences in theoretical and practical grounds. Knowledge of population dynamics is central to the analysis of life history variation and to the understanding of the selective factors acting in the different stages of the life cycle (Stearns 1992); it is also relevant in the design of plans aimed at the conservation of rare species, the control of invasive species and the design of sustainable harvesting programs (Horvitz and Schemske 1995).

Matrix population models are particularly useful for studying population dynamics, as they incorporate the quantitative demographic data that describe the life cycle of a population with age or stage structure, and produce various measures of population growth, structure and behaviour which may be compared between species or between population of the same species (Caswell 1989,

Silvertown et al. 1993). For plant populations, the Leftkovitch projection matrix, in which individuals are classified according to size or developmental stage, has been widely used. This method allows the modeling of the complex life cycles that characterize most plant species and is well suited for organisms whose demographic behaviour is more closely related to size than to age of the individuals (Werner and Caswell 1977, Fiedler 1987, Valverde and Silvertown 1998).

Many studies with projection matrices explore the consequences of population dynamics for the conservation of rare species (Crouse et al. 1987, Lande 1988, Menges 1990, Boyce 1992, Durán and Franco 1992, Ferriere et al. 1996), or the impact of different harvesting regimes (Peters 1990, Pinard 1993, Olmsted and Alvarez-Buylla 1995, Ratsirason et al. 1996, Bernal 1998). However few, if any, have addressed the impact of different management practices designed to restore (or reintroduce) a population in a disturbed area.

In this paper we study the population dynamics of an oak population in order to: a) evaluate its present state, b) explore the potential impact on population growth of alternative management practices, and c) discuss alternative restoration practices in view of the above. We start by building population projection matrices form observations made during a six-year in a natural *Quercus rugosa* population, then we present model simulations to evaluate the impact of different restoration practices on population growth.

Methods

Study site

The study was conducted at the Parque Ecológico de la Ciudad de México, a recently protected area located at the piedmont of the Ajusco hills, south of Mexico City. Mean annual temperature is 15°C and mean annual rainfall is 1000 mm. There are three main types of vegetation at the park: an oak-pine forest in the higher parts (at a mean altitude of $\approx$ 2800 m), an oak forest at an intermediate altitude ($\approx$ 2500-2700 m), and a shrubland at medium and lower elevations (2400-2600 m). The last two types or vegetation are closely associated with edaphic conditions, as the closed oak forest is located mainly on hills with well developed soils (mainly eutric cambisol), while in the lower parts, which were covered by lava flows from the nearby Xitle cone around 2000 years ago, a rock bed of andesitic-basaltic composition prevails (Cordova et al. 1994). The low water retention capacity of the basaltic rock has induced the establishment of a shrubland dominated by xeric species, mainly *Opuntia* spp., *Agave* spp., *Senecio praecox* and *Sedum oxypetalum*. This shrubland

was formerly dominated by sparse trees of *Quercus rugosa*, while in other patches an open woodland of *Quercus rugosa* and/or *Quercus castanea* was present.

As a result of a severe disturbance created by a temporary human settlement established in 1988, the vegetation was eliminated and the basaltic rock exploited in order to use it as building material. This eliminated the oaks and created favorable conditions for the establishment of species characteristic of disturbed sites, mainly *Buddleia cordata* and *Dodonea viscosa*, as well as several species of annual herbs.

The ecological restoration of the site started in 1990, and one of its main goals was to reintroduce the oaks in the disturbed area (Bonfil et al. 1997). As a result, several studies were initiated with the idea of gaining insight on the conditions favoring oak establishment and growth. Knowledge of the population dynamics of the main oak species under natural conditions was considered essential to meet this end.

The species

Quercus rugosa is a white oak (Leucobalanus) that has a wide distribution in México (occurs in 26 out of 30 states where oaks are present, González-Rivera 1993). Adults are around 10-20 m tall (up to 30 m), and have thick and rigid leaves that are partially shed in December. It is found at altitudes between 1800 and 2880 m above sea level, either forming pure stands or intermingled with other oak and pine species (González- Villarreal 1986).

Population sampling

The study site was extensively surveyed at the beginning of 1991. As oak regeneration is concentrated on a strip corresponding to the forest border (i. e. the transition between the closed forest and a more open shrubland, Bonfil and Soberón 1998), a 300 x 10 m transect was established along the border in May 1991, and all seedlings, saplings and young and mature trees of *Q. rugosa* within this area were tagged and located on a map. Height, trunk basal diameter and crown area of each individual (except mature trees) were recorded. In the case of adult trees all individuals on the transect, as well as those located in an adjacent area of 0.75 ha (from the border into the forest) were tagged, and height and diameter at breast height (dbh) of each trunk were measured.

In order to construct a projection matrix model, data on the fate of individuals (i. e., whether a plant died, remained in the same size category, grew or diminished in size) were collected. All individuals within the area of the transect, as well as new recruits, were registered and measured again in May 1992, 1993 and 1994. A subsample of the adult trees in the 0.75 ha was re-measured in 1992. Since no noticeable change in dbh was detected on this period, and in order to detect some increment, the trees were measured again five years later (1997). As trunks are straight, dbh data were used to calculate basal area. The woodland had been logged during the first decades of this century to produce charcoal, and as a consequence a high proportion of trees consist of several stump-sprouts, so the basal area of each tree was considered as the sum of the basal areas of its sprouts.

Population structure

Individuals were classified according to size in seven categories (Table 1). The pre-reproductive categories were classified by height (except seedlings, see below), while adults were classified according to basal area. The transition between the last category based on height (J 2) and the first based on basal area (A 1) was made considering that a 3 m tree, which would correspond to the lower height value of Adults 1, has a mean basal area of 80 cm^2, and this was taken as the lower limit for individuals in this category. It is also the size at which individuals become reproductive. This classification includes all plants in a continuum gradient of sizes and prevents overlapping sizes.

Fecundity was estimated by recording seedling recruits, instead of number of seeds produced, due to the fact that the acorns, which are released between October and November, germinate readily if enough moisture is available, and do not remain viable in the soil for long. This constrains the formation of a seed bank, and non germinating acorns either are predated or lose viability within 2-3 months after being shed. The identification of newly recruited seedlings can be difficult, because oak seedlings are capable of resprouting after aerial biomass death, so height is not a good indicator of age (Merz and Boyce, 1956). In cases where the seedling was still attached to the acorn the identification was straightforward, and when the acorn was missing the diameter of the root collar, along with careful observation, was used as a clue. Previous data of nursery-grown seedlings at the study site had shown that the root collar diameter of 5-6 month old seedlings (which could be the oldest possible age of new seedlings at the time when observations were made) is ≤ 2.5 mm, and these data were used to distinguish new recruits from older resprouts.

Die-back or death of the apical portion of the shoot and branches is common in oaks, which resprout from dormant buds after top kill (Crow 1988). As a consequence of shoot die-back, juveniles can decrease in height and move to a lower size class. However, saplings cannot become

4

seedlings as a result of die-back, and thus they include individuals whose root collar is >2.5 mm, and can go from a few centimeters to 50 cm tall.

Population Projection Matrix

a. The Model

The Lefkovitch matrix, in which individuals are classified into size or stage categories, has proved to be particularly useful in studies of plant demography (Werner and Caswell 1977, Silvertown et al. 1996, Valverde and Silvertown 1998). The basic matrix model is:

$$n_{t+1} = \mathbf{A}\, n_t$$

in which n_t and n_{t+1} are column vectors whose elements are the number of individuals in each category at times t and $t+1$, respectively and $\mathbf{A}$ is a square non-negative matrix whose elements (a_{ij}) are the transition probabilities among categories in one time period, i.e. the contribution of individuals of category j to category i in the time interval form t to $t+1$ (in this case a year). The Lefkovitch model allows transitions in which individuals either remain in the same category, move forward one or more size categories (by growing), go back to lower size categories (decrease in size), and reproduce either sexually (by seeds) or asexually (vegetative propagation) and thus is ideal for plant populations, in which size may be more important than age in order to predict the fate of an individual. By using this model it is possible to project the future size of the population given that conditions remain stable, and therefore matrix $\mathbf{A}$ is known as the projection matrix.

The methods explained in Caswell (1989) were used to estimate the population growth rate (λ), the stable size class distribution ($\mathbf{w}$) and the reproductive value distribution ($\mathbf{v}$), which correspond to the dominant eigenvalue of the matrix and its associated right and the left eigenvectors, respectively The stable size distribution ($\mathbf{w}$) is a vector that shows the proportion of individuals that would belong to the different size classes at equilibrium, i. e. when the population is growing at a constant rate λ. The reproductive value distribution ($\mathbf{v}$) is a vector that shows the class- specific reproductive values, which are a standard measure of the offspring contribution of an average individual in each class, i. e. the value of an average individual in each size-class in terms of the number of offspring that it is expected to produce.

A 7 x 7 matrix was built in which the number of columns/rows was given by the number of size classes used. Data on proportions of individuals entering, staying and leaving each size category

from one year to the next were averaged for the three-year period in which pre-reproductive size classes were followed.

b. Fecundity

Fecundity was estimated as mean number of seedlings produced by an adult of a given size class. Although the total number of annual recruits was known, there were no data available on the exact reproductive contribution of each of the three categories considered (A1, A2 and A3), and hence two matrices, differing only in the assignment of fecundity contributions, were made in order to evaluate the impact of these different assumptions on population growth.

In the first case, a weighed contribution was made in which young adults (A1) were arbitrarily assigned a proportional reduction of 0.33 in relation to the contribution of Adults 2, while in Adults 3 this reduction was .08, i. e. the contribution of an individual Adult 3 was 92% that of an Adult 2. In the second case, Adults 1 were assigned half the reproductive contribution of the other two adult categories, which did not differ. These calculations were based on field observations over a six-year period, which had shown that young adults have a lower and more erratic seed production than older adults, which have a similar seed production once they have achieved a certain threshold size, except perhaps for the oldest individuals, whose seed production may decrease.

c. Survival and growth

In most cases transition probabilities were calculated according to the observed proportion of individuals moving from one class to the next in one year. However, in some classes no individuals moved to any other class (i.e. Juveniles 2→ Adults 1); in these cases individual growth rates were calculated and average annual growth of the individuals in a given category was used to estimate transition probabilities (Enright and Ogden 1979). This was done by calculating the number of years necessary for a mean individual starting at size x (the initial size of the class) to reach size x+1 (the initial size of the next category). The inverse of this quantity multiplied by the survival probability was assumed to represent the expected transition probability in a year, while the probability of remaining in the same class was obtained by subtraction once the transitions were known.

To estimate the transitions for Adults 1 and Adults 2, individual annual growth rates for these trees were calculated from the increment in basal area detected over a six-year period (1991-97). A positive correlation was found between annual increase in basal area and initial basal area of each tree. This relationship was best explained by the equation

log increase = 0.7477 + 0.00864 basal area

which was used to calculate the new size individuals would attain in a year, and from these data transition probabilities were estimated. The regression is highly significant ($R^2 = 0.722$, $F = 106.38$, $P < 0.001$) and applies to trees growing at the forest border, as in other conditions growth may differ.

As no deaths were recorded in the largest adult category (A3), survival rates were calculated by using the program of Cochran and Ellner (1992), and finding the survival rate that would render a lifespan of 130-140 years, which corresponds approximately to the estimated age of the oldest trees in the area.

d. Estimating transitions through individual growth rates and simulations

In addition to the matrix with the observed transition probabilities for the pre-reproductive size classes (M1), another matrix was built using transition probabilities calculated from mean individual growth rates, as described, for all pre-reproductive classes, except seedlings (in which all survivors move to the next class). This new matrix M2 was constructed with the aim of comparing the results obtained by the two methods used to estimate transition probabilities as a way to analyze the impact of estimations based on mean individual growth rates

If the matrix M2 produces similar results to matrix M1, then the impact of modifying individual growth rates on population growth could be assessed by modifying the entries of the second matrix. By this means it is possible to evaluate the impact that different management practices, designed to increase individual growth rates, would have on population growth.

e. Sensitivity and elasticity analyses

Sensitivity and elasticity analyses were used to measure the impact that small changes in growth, survival and fecundity have on the value of λ. Sensitivity values estimate the sensitivity of λ to changes in the elements of the matrix, and it is the partial derivative of λ with respect to an infinitesimal change to each matrix entry:

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\mathbf{w} \bullet \mathbf{v}}$$

where v_i and w_j are the ith element of the reproductive value vector and the jth element of the stable stage distribution, respectively, and $\mathbf{w} \bullet \mathbf{v}$ represent the scalar product of the two vectors (Caswell, 1989). However, as transition probabilities and fecundities are measured on different

scales, comparison of their sensitivities may be difficult, and in order to overcome this difficulty de Kroon et al. (1986) developed the elasticity concept. Elasticities are dimensionless sensitivities normalized for comparison among traits measured in different units (Stearns, 1992). Elasticity is calculated by the formula

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = S_{ij} \frac{a_{ij}}{\lambda}$$

which gives the proportional change in λ resulting from a proportional change in a_{ij} (Caswell, 1989). As the sum of all the elasticities in a matrix equals unity, each e_{ij} can be interpreted as the relative contribution of each a_{ij} to λ.

Results

Population structure and projection matrix model

The structure of the oak population studied shows that the highest proportion of individuals correspond to the sapling stage with 35% of the population, while the three adult stages comprise 30% (Fig 1). This structure corresponds to the oak population at the forest border, in which adult density is 250 ind/ha., while in other areas, like the forest interior, there are higher adult densities and few pre-reproductive individuals present.

The projection matrix M1, with the observed transition probabilities, is shown in Table 2a. It can be seen that mortality decreases with size, from an annual rate of 39% for seedlings to 2% or less for adults.

The annual seedling production is relatively low, with less than one seedling per adult tree (mean = 21 seedlings in 3 000 m², N =15, 31 and 18 recruits in 1991, 92 and 93, respectively). Although the number of germinated acorns is usually higher, successful recruitment of seedlings is low due to high acorn and seedling mortality during the first part of the year, particularly in the dry months of January-March (Bonfil and Soberón 1998). Seedlings alive in May (when the censuses were made), have a mean survival rate of 0.61, varying from 0.45 to 0.72 over the three year period.

At the sapling stage, growth is restrained by the high proportion of suppressed individuals (Table 3), which do not grow or even decrease in height due to repeated die-back. A suppressed sapling may remain in this class for many years, although in good growing conditions may attain more than 50

cm in 4 - 5 years, considering a mean height of 15 cm when leaving the seedling stage. This restrained growth is found in all pre-reproductive classes, although as individuals progress to larger size classes suppression diminishes (Table 3) until in the adult stages individuals are not suppressed at the densities found at the forest border. This suppression, coupled with the low growth rate characteristic of the species, must have important consequences for population growth.

According to the model, the population is close to equilibrium and will grow very slowly under the present conditions, at an annual rate of 0.35 %. The observed population structure and the stable stage distribution (w) were similar and did not differ significantly (log likelihood ratio G = 0.037, d.f. 6, P = 0.98, Fig. 1).

The second matrix (M2), in which the probabilities of remaining in the same category or passing to the next one for pre-reproductive size classes (except seedlings) were calculated from mean individual growth rates (Table 3b), produced similar results to those obtained with matrix M1, except for a small reduction in λ, which changed from 1.0035 to 1.0016. Stable stage distributions, stage-specific reproductive values and the elasticity matrices were similar in both cases (Table 2). This implies that using either the observed transitions for the pre-reproductive stages, or the calculated ones through knowledge of individual growth rates renders similar results and suggests that the latter is a good estimate of what actually takes place in the population.

The two different fecundity assignments made did not produce an important change on λ, as the value obtained by using the second alternative (fecundity of Adults 1 being half of that of Adults 2 and 3, which was equal, see Fecundity in the Methods section) was very similar to the λ value obtained with the original matrix M1 (1.0034 vs. 1.0035, respectively).

The elasticity matrix obtained from matrix M1 (Table 2c) indicates that population growth rate depends mainly on stasis (i. e., individuals surviving and remaining in the same category), which accounts for 91% of the value of λ, with adult stasis being particularly important (68%). On the contrary, the contribution of the fecundity elements to λ is low, accounting for 1% of the λ value. Retrogression accounts for only 0.8%, and growth as a whole contributes with 7%, with the transitions sapling→juvenile 1 and juvenile 1→juvenile 2 having a larger contribution than the rest of them. The elasticity matrix obtained from transition matrix M2 was similar to that obtained from M1, with practically the same relative contributions from fecundity, stasis, retrogression and growth (Fig.2).

Simulations

As matrix M2, constructed from data on individual growth rates, produced similar results to matrix M1, the first was considered as a conservative model that could be used to explore the effects of changing the entries of the matrix (a_{ij}), on population growth rate. The aim of these simulations was to explore which management practices, designed to increase individual growth, would have the effect of increasing population growth rate and thus potentially contribute to oak recovery at the site.

The effect of reducing the proportion of suppressed individuals in pre-reproductive size classes, which would result in an increase of the average individual growth rate of each class, was evaluated both by changing each matrix entry individually and by modifying more than one simultaneously. This would represent management conditions given by selective removal of tree branches and shrubs, i.e. clearing and pruning practices that could eliminate suppression in varying proportions of individuals of each size class. In the simulations, the observed proportion of suppressed individuals in the sapling, juveniles 1 and juveniles 2 categories (Table 3) was reduced by 1/3 and 1/2 of their original value, and the resulting mean individual growth rate for each category was used to estimate the new transition probabilities and its associated λ value (Table 4). In the case of juveniles, the reduction in the proportion of suppressed individuals was considered as having an effect on: a) permanence and progression probabilities only, and b) decreasing retrogression probabilities as well (i.e. reducing die-back; see asterisks in Table 4).

The impact on λ of reducing the proportion of suppressed individuals by 1/3 in any one of the three categories considered is rather small, and in this case the best results are achieved by reducing the suppression of juveniles 1, which would increase annual population growth from its original 0.16% to 0.43% (Table 4b). A suppression reduction of 1/2 has a larger impact on every category, and in this case the sapling category renders the largest increase in λ, by shifting population growth rate to 0.71% (Table 4a). However, if the reduction of suppression by half is associated with a similar decrease in die-back, which is a realistic assumption, the result obtained with saplings would be very similar to the one obtained with juveniles 1 (0.71 and 0.73%, respectively).

When 1/2 of juveniles 1 and juveniles 2 simultaneously are released from suppression (Table 4d), annual growth rate increase to 0.75%. This is further increased to 1.15% when retrogression is also diminished. Only in the latter case there is a noticeable difference from concentrating efforts in saplings or juveniles 1 alone. Finally, if all sapling and juvenile categories were to be managed (Table 4e), the population growth rate could be increased to 1.08% (with a 1/3 reduction in suppression), to 1.42% (with a 1/2 reduction), or to 1.85% if there is an additional 1/2 reduction in retrogression, respectively.

An alternative management practice that could have an effect on population growth rate is to increase seedling input, which in the context of the model is equivalent to increasing fecundity. If it is assumed that the original values of the fecundity entries of matrix M2 could be doubled (by sowing germinated acorns or planting young seedlings), the simulation predicts an annual growth rate of 1% (Table 5a). This could be achieved by changing mean annual seedling input from 21 to 42 seedlings (in the sampled area; 70 - 140 seedlings ha^{-1}) . If this value could be further increased to 65 individuals (203 seedlings ha^{-1}) recruited annually (which implies modifying the fecundity entries of Matrix M2 to 0.5, 1.0 and 1.0 for Adults 1, 2 and 3, respectively, Table 5a), then a population growth rate of 1.6% is predicted by the model. Finally, in order to further increase population growth rates, the increases in seedling input could be combined with the clearing and pruning practices that reduce suppression by half in the three pre-reproductive categories. Under these management practices, the annual population growth rates obtained by doubling seedling input would be between 2.8% and 3.4%, while the larger seedling input would produce a population growth rate of 4.3% or 3.36%,depending on whether retrogression is affected or not (Table 5b).

As high elasticities are linked to adult stasis (Table 2c), the impact on λ of changes in adult survival was assessed by modifying the proportion of adults remaining in each category. The results (Fig. 3) show that a slightly lower value of adult stasis than the one originally included in the corresponding matrix, which is equivalent to an increased mortality, is associated with a decrease in λ, while mortalities higher than 3% for Adults 3 and higher than approximately 7% for Adults 2 and Adults 1 produced λ values < 1, and therefore would cause population decline.

Discussion

The results show that if current conditions were to be maintained for a long time, the oak population at this site would remain stable. This demographic behaviour is given both by the characteristic morphological growth pattern of the species (oaks have a semideterminate growth, which is restricted to one or a few flushes per season; Reich et al. 1980, Hanson et al 1986) and by the restrictive conditions found at the site. Although no other study of oak population dynamics has been published, it is known that many oak species have low individual growth rates, and various studies are aimed at improving oak regeneration, which is absent or scarce in many areas (Ovington and MacRae 1960, Shaw 1968, Griffin 1970, Gottschalk 1985, Espelta et al.1995, Thadani and Ashton 1995).

The finite rate of increase found for this population is among the lowest values reported, if compared with other tree and palm species (Table 6). The λ values reported here correspond to the

population dynamics at a transition site, i.e. the forest border. However, as this is the area where regeneration is taking place, the maintenance of the population depends on the dynamics found in it. A similar situation has been described by Enright (1982) for *Araucaria hunsteinii*, whose relevant population growth occurs in forest gaps. In the case of *Q. rugosa* there is no regeneration in the forest interior because, although seedlings are able to establish, they do not survive long and consequently the sapling and juvenile stages are not represented. Conversely, seedlings are not able to become established on completely open conditions, and this limits the rate at which oaks can invade the disturbed shrubland (Bonfil and Soberón, 1998).

Taken on a long time scale, the growth of this oak population can be seen as part of a succesional process, in which oaks are slowly invading the contiguous shrubland area. As individuals on the present forest border grow, the canopy closes at the forest border and regeneration is restricted to the expanding outer portions of the forest. The colonization of this shrubland by oaks under natural conditions will proceed in steps related (but larger than) the time elapsed between seedling establishment and attainment of the reproductive stage, which takes 30-40 years. (Age to maturity 28 years; mean age of Adults 1: 45 years, both calculated with Cochran and Ellner's 1992 program). A similar invasion of heathland by oak shrubs has been described by Jensen and Nielsen (1986).

The restrictive conditions for establishment given by the basaltic substrate, the lack of soil and the scarce vegetation at the disturbed area (Bonfil and Soberón 1998) further slows the invasion by oaks. Growth of the population relies on the amelioration of these conditions by the shade and litter produced by adult trees. Population growth is therefore closely tied to the forest border, although it could occur also at other sites, such as forest gaps. Even under these conditions seedling establishment is not widespread, as judged by the annual seedling input rates found during the study period. This low establishment is not due to a shortage of seeds, as this species produces abundant annual seed crops (though masting is also common), but rather to a combination of high seed predation and scarcity of suitable microsites for germination and early seedling survival.

In relation to parameter estimations, it must be recalled that although our estimate of fecundity was based on qualitative field observations (and therefore the exact contribution of each category was arbitrarily assigned), this did not have a noticeable impact on the λ value obtained, as the two different assignments of fecundity rendered similar results. This low impact on λ of different assumptions of fecundity contributions was also found by Enright (1982) for *Araucaria* species. Our assumptions of fecundity changing with size (age) are supported by the results of Downs and McQuilkin (1944), who also found a comparatively low acorn production in the smaller reproductive classes of five oak species, and a rising production that either leveled off or declined in the largest trees, depending on the species.

The need to average mortality and growth data for the study period arose from the low mortality and growth rates of adults, which made necessary an observation period much longer than a year in order to obtain reliable data on these vital rates. This constrained the possibility of between-year comparison on population growth rates. Therefore, the most important yearly variations detected corresponded to seedling recruitment and survival, which are linked to weather conditions, especially to the amount and distribution of winter rains. Nontheless, the variation in the number of seedlings recruited per year during the three years of study was not very high (see for example Horvitz and Schemske 1995), though it is possible that significant variation in this parameter might only be detected over longer time scales.

At the forest border most seedlings were located under established trees or shrubs, which explains the high proportion of suppressed saplings and the low average annual growth rate registered for this category. The long period of time that a plant can remain in the sapling stage causes both a high relative proportion of individuals at this stage (Fig. 1), and a high relative contribution of saplings to the population's growth rate. The lack of difference between the observed population structure and that expected at the stable stage distribution may indicate the absence of important disturbances at the forest border in recent times. According to local informants, this portion of the forest has not been logged at least for the last 50 years.

To date, most of the applications of plant demographic studies have been directed to project numerical changes in populations exposed to harvesting (i.e. Peters 1990, Pinard 1993, Gingsberg and Milner-Gulland 1994, Olmsted and Alvarez-Buylla 1995, Ratsirason et al. 1996, Bernal 1998), and thus design sustainable harvesting regimes, while their use in designing plant reintroduction and restoration strategies has been less common, except in the context of the analysis of endangered species (Crouse et al. 1987, Lande 1988, Menges 1990, Aplet et al. 1994, Heppell et al. 1996, Ferriere et al. 1996). The simulations presented in this study were carried out in order to explore the effectiveness of different management practices in increasing population growth rate (Silvertown et al. 1996), and thus on a perspective of "accelerating" succession (Luken 1986) by reintroducing a previously dominant tree species in a disturbed shrubland.

A management practice that would result in the release of the growth of variable proportions of individuals in each category by clearing and pruning practices was considered due to its applicability, as it is feasible that between one third and one half of the suppressed saplings or juveniles can gain access to higher light levels by selective removal of branches of established trees or shrubs that keep them in shaded conditions. It is less practical to pretend releasing higher proportions of individuals in these categories, as this would involve releasing those placed under a thick canopy. The results of the simulations show that these practices have a limited effect on increasing λ when they are focused in only one size class, as in no case population growth rate could be brought to 1%

per year. Therefore, a better strategy, although more labor-consuming, would be to release either one half of all juveniles (J1 + J2) or between a third and a half of all saplings and juveniles, as in these cases the resulting annual population growth rates would be higher than 1%.

In case of releasing half of the suppressed juveniles, two scenarios were considered: affecting only stasis and progression probabilities or decreasing shoot die-back and hence diminishing retrogression probabilities. The latter seems more likely, as death of the apical portion of the shoot is closely associated to shaded conditions (but there are other agents causing reductions in height i.e. herbivores, drought), and therefore individuals in favourable light conditions should suffer less from shoot die-back. If this is the case, releasing half of the suppressed saplings and juveniles would have an important effect on population growth, as the growth rate would be close to 2%, which represents a considerable increment in relation to the original 0.16%.

Although high elasticities were associated with adult stasis, as reported for other trees (Caswell 1986, Silvertown et al. 1993) it is not easy either to improve growth rates or survival in the case of adults. The mortality rates found are already low (Table 2a) and the individual growth rates reported correspond to the low adult densities registered at the forest border, while in more crowded conditions they are lower. Simulations of increasing mortality probabilities showed that λ was indeed very sensitive to changes in adult survival (Fig 3). Although this could be taken as an indication of the susceptibility of the population to harvesting of adult trees, and therefore could suggest to forbid logging in similar areas, it is known that Q. rugosa, as most oaks do, produce stump sprouts in case of stem cutting (Roth & Hepting 1943, Reich et al 1980, Retana et al. 1992, Crow 1988, Dey et al. 1996). As a consequence, these simulations are useful only for projecting changes due to increased mortality, and an experimental study specifically designed to evaluate sprouting and growth responses of adults of different sizes to stem cutting is needed before any recommendations related to logging can be made. It is to be expected, however, that the low individual growth rates of adults should limit the usefulness of harvesting.

The results obtained by the alternative simulated practice of increasing seedling input appear promising. The number of planted seedlings that would be required to produce the fecundities used in the simulations is relatively low, and in case of attaining 203 seedlings ha^{-1} (i.e. fecundities of 0.5, 1 and 1 for A 1, A 2 and A 3 respectively), the λ value obtained is similar to the one that would be achieved by clearing and pruning practices releasing half of the suppressed saplings and juveniles. Seedling planting is a standard management practice, and although mortality of young seedlings may be high in bad years (i.e. those with a severe dry season), previous studies (Bonfil and Soberón 1998) have identified the microsite conditions conductive to high survival. Planned, careful planting can be easily devised to achieve the desired seedling establishment. The introduction of acorns is

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not recommended in view of the high acorn losses previously detected at the site (Bonfil and Soberón 1998).

Given the low elasticity values associated to fecundity, the above results may seem odd. Nevertheless, it should be considered that the high elasticities associated to adult stasis describe the behaviour of a population that sustains itself due to survival of adult trees (de Kroon et al. in preparation), while the goal of the simulations was to explore the effect of different management practices designed to improve population growth. As the values of fecundity are less bounded than those transitions describing stasis or growth (in which the addition of all transitions in a column may not exceed unity), the changes made when modifying the former were proportionally much higher than the ones that can be made with either pre-reproductive size classes or adults, and had a large impact on λ. Therefore, efforts directed at improving reproduction seem promising, and the results attained reinforce the view that elasticities should not be used as the only reliable guide for practices aimed at conservation (Silvertown et al. 1996, de Kroon et al. in preparation).

Finally, the inclusion of both selective pruning practices and planting of seedlings is advised in an oak restoration program, which, according to our results, would render a maximum annual population growth of 4.3%. Pruning has the advantage of releasing the growth of individuals that are already well established and therefore acclimated to prevailing conditions, and allows a more rapid increase in the number of adult trees. Additionally, if each seedling is carefully placed on appropriate light conditions, the need for future intensive clearing an pruning practices will probably decrease. The λ value obtained even under these conditions, however, is not particularly high in relation to other reports, and the simulations revealed that the demographic behaviour this oak population is not flexible. In view of the overall results, a conspicuous expansion of the oak population into the disturbed zone is not to be expected in the short term, and this should be taken into account when designing the restoration program for the area.

Table 1. Classification of individuals in size categories

HEIGHT		BASAL AREA	
Seedlings	new recruits	Adults 1	≥ 80 and < 350 cm^2
Saplings	1-50 cm	Adults 2	≥ 350 and < 750 cm^2
Juveniles 1	≥ 50 cm and less than 1 m	Adults 3	≥ 750 cm^2
Juveniles 2	≥ 1 m and less than 3 m		

Table 3. Mean growth rates and proportion of suppressed individuals in pre-reproductive categories

Stage	growth rate (cm year^{-1})	% suppressed
Saplings	2.2	49
Juveniles	15.4	42
Juveniles 2	12.0	28

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Table 2. a) Transition matrix from observed data b) Transition matrix from calculated data, and c) Elasticity matrix corresponding to transition matrix 1. Categories as shown in Table 1. Mortality and initial number of individuals are the same in a and b (q_x = mortality, w = stable stage distribution, v = reproductive value distribution)

a) Transition Matrix M1 (obs) λ = 1.0035

	seedl	sap	J1	J2	A1	A2	A3	w	v
seedl	0	0	0	0	0.21	0.32	0.295	.069	.016
sap	0.613	0.859	0.08	0	0	0	0	.397	.027
J1	0	0.082	0.789	0.097	0	0	0	.192	.047
J2	0	0	0.089	0.808	0	0	0	.088	.089
A1	0	0	0	0.052	0.951	0	0	.087	.247
A2	0	0	0	0	0.0306	0.9491	0	.049	.311
A3	0	0	0	0	0	0.0447	0.985	.118	.261
q_x	0.387	0.059	0.042	0.043	0.018	0.006	0.015		
N	21	91	50	24	20	23	32		

b) Transition Matrix M2 (calc) λ = 1.0016

	seedl	sap	J1	J2	A1	A2	A3	w	v
seedl	0	0	0	0	0.21	0.32	0.295	.068	.014
sap	0.613	0.879	0.08	0	0	0	0	.445	.024
J1	0	0.061	0.784	0.097	0	0	0	.159	.048
J2	0	0	0.094	0.808	0	0	0	.077	.091
A1	0	0	0	0.052	0.951	0	0	.079	.249
A2	0	0	0	0	0.0306	0.9491	0	.046	.312
A3	0	0	0	0	0	0.0447	0.985	.124	.261

c) Elasticity Matrix (obs)

	seedl	sap	J1	J2	A1	A2	A3
seedl	0	0	0	0	*0.0031*	*0.0026*	*0.0059*
sap	0.0116	**0.0945**	0.0042	0	0	0	0
J1	0	0.0159	0.0737	0.0041	0	0	0
J2	0	0	0.0158	0.0657	0	0	0
A1	0	0	0	0.0116	**0.2112**	0	0
A2	0	0	0	0	0.0086	**0.1495**	0
A3	0	0	0	0	0	0.0059	**0.3156**

Table 4. Effects of reducing the proportion of suppressed individuals on population growth rate (λ).

Size class	Prop. suppressed	Suppression Reduction	Resulting prop. suppressed	λ
a) Saplings	0 .49	1 /3	.32	1.0018
		1 /2	.245	1.0071
b) Juveniles 1	0 .42	1 /3	.28	1.0043
		1 /2	.21	1.0054
		1 /2*		1.0073
c) Juveniles 2	0 .285	1 /3	.19	1.0029
		1 /2	.145	1.0034
		1 /2*		1.0057
d) J1 + J2		1 /2		1.0075
		1 /2*		1.0115
e) Sap + J 1 + J 2		1 /3		1.0108
		1 /2		1.0142
		1 /2*		1.0185

* indicates an additional reduction of 50% in retrogression.

Table 5. Effects of: a) increasing seedling input and, b) increasing seedling input and reducing the proportion of suppressed individuals by half on population growth rate (λ).

	Size class	Fecundity	Suppression Reduction	λ
a)	A1	0.42		
	A2	0.64		
	A3	0.59	0	1.0104
	A1	0.5		
	A2	1.0		
	A3	1.0	0	1.0165
b)	A1	0.42		
	A2	0.64		
	A3	0.59	½	1.0283
			½*	1.0341
	A1	0.5		
	A2	1.0		
	A3	1.0	½	1.0336
			½*	1.0430

* indicates an additional reduction of 50% in retrogression.

Table 6. λ Values previously reported for other tree and palm species

Palms

Astrocaryum mexicanum	1.0046 (0.9932-1.0399)	Piñero et al., 1984
Coccothrinax readii	1.0549	Olmsted & Alvarez-Buylla, 1995
Chamadorea tepejilote	0.9699 - 1.1232	Oyama, 1987
Iriartea deltoidea	0.9894-1.0166	Pinard, 1993
Phytelephas seemannii	1.0589	Bernal, 1998
Podococcus bartieri	1.0125	Bullock, 1980.
Pseudophoenix sargentii	1.0009-1.1995	Durán and Franco, 1992
Reinhardtia gracilis	1.0123-1.0396	Mendoza, 1994
Thrinax radiata	1.0925-1.1492	Olmsted & Alvarez-Buylla, 1995

Non-palm species

|		
Araucaria cunninghamii	1.0204	Enright & Ogden, 1979
Araucaria hunsteiinii	1.065	Enright, 1982
Beilschmedia tawa	0.9990-1.0228	West, 1995
Brosimum alicastrum	1.0635	Peters, 1971
Cecropia obtusifolia	0.9720	Alvarez-Buylla, 1986
Grias peruviana 1.018		Peters, 1990.
Nothofagus fusca	1.0100-0.0996 1.0279-1.0095 1.0171-1.0029	Enright & Ogden, 1979
Pentaclethra macroloba 1.002		Hartshorn, G. 1975
Quercus rugosa	1.0035	This study
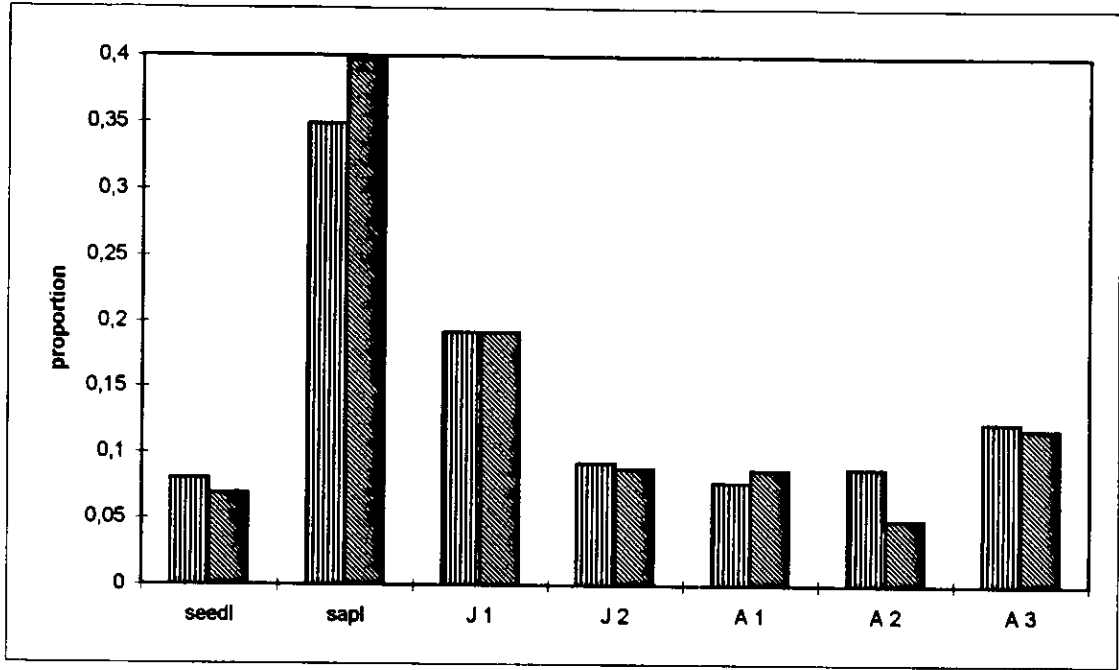
Fig 1
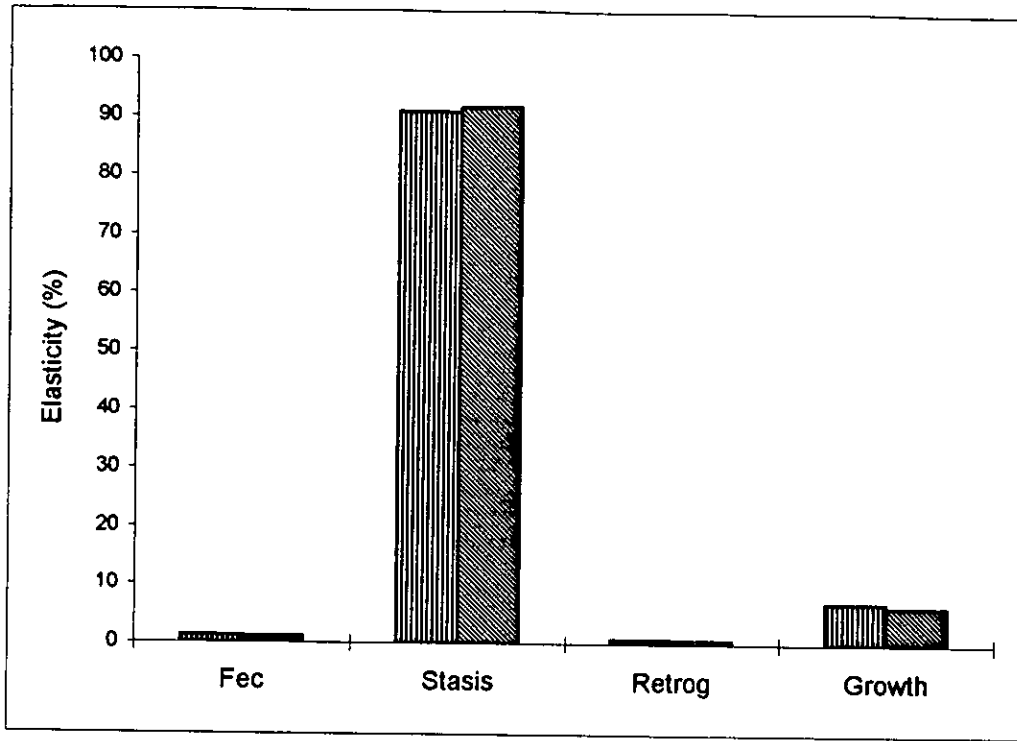
Fig 2
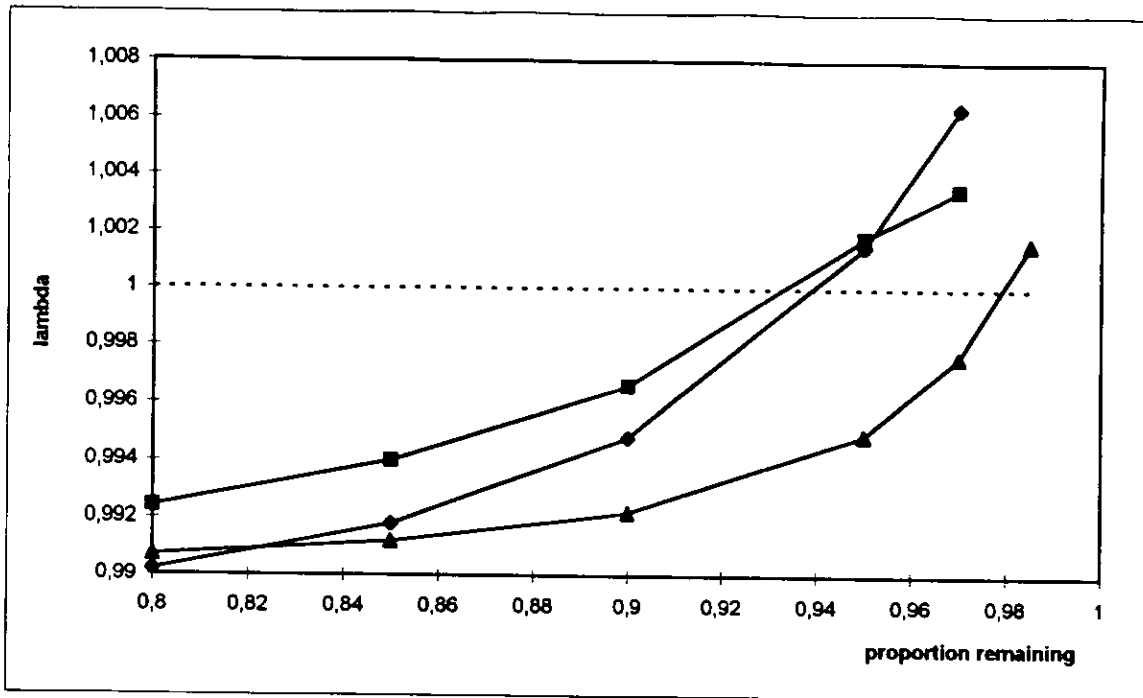
Fig. 3

Figure legends

Fig. 1. Observed (left side) and expected (right side) stable stage distribution of the studied oak population. Stages as described in Table 1.

Fig. 2. Percentage elasticity corresponding to fecundity, stasis, retrogression and growth. Right hand side: matrix M1, left-hand side: matrix M2.

Fig. 3. λ values associated to varying proportions of adult permanence ($\blacklozenge$ = Adults 1, $\blacksquare$ = Adults 2, $\blacktriangle$ = Adults 3). The observed values correspond to the last value for Adults 3, and second-to last for Adults 1 and 2.

CAPÍTULO V

CONCLUSIONES
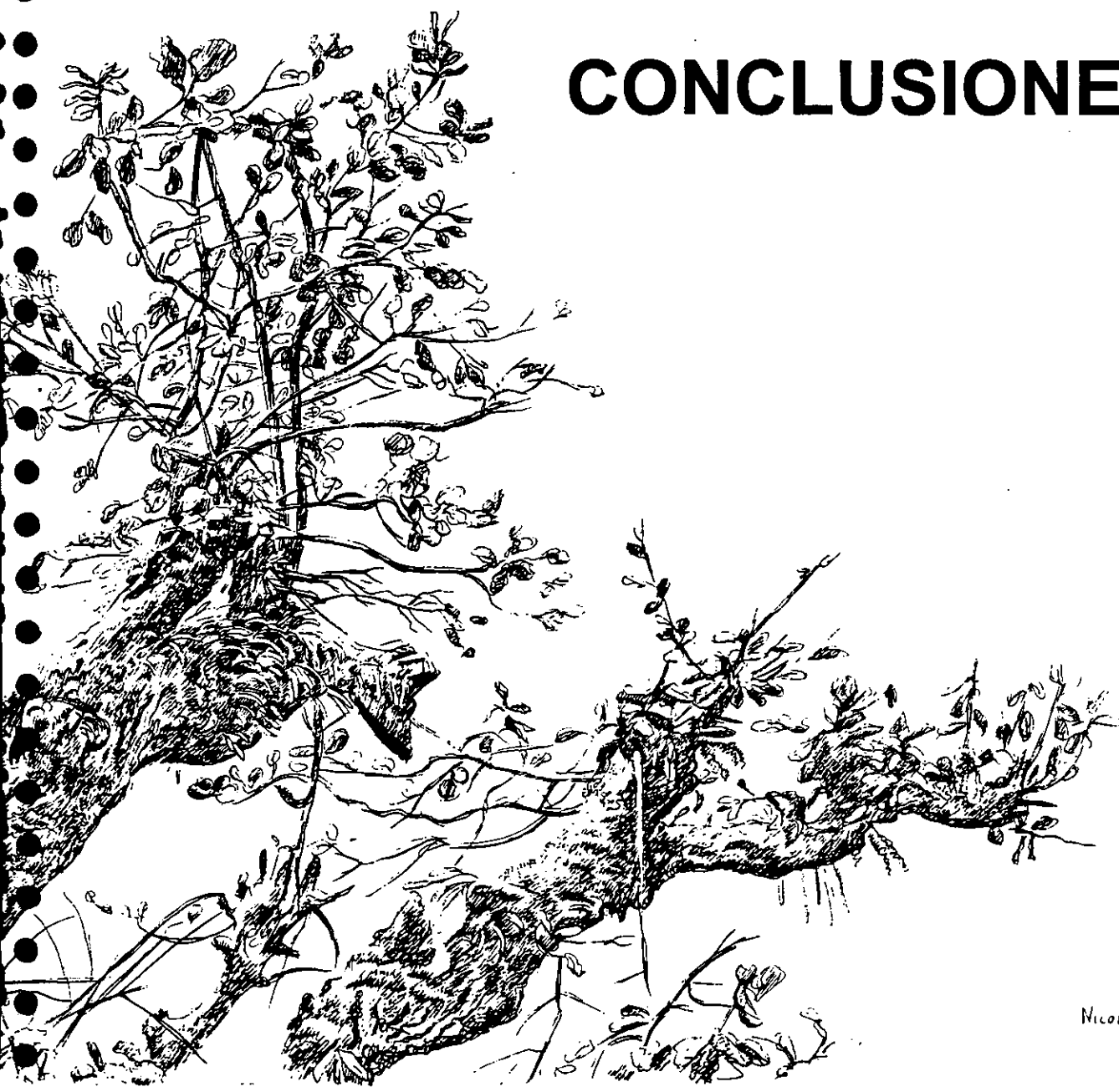
Nicolas Moreno
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Conclusiones

El análisis de la regeneración y la dinámica poblacional de *Quercus rugosa* fue el eje principal en torno al cual giraron las investigaciones incluidas en la presente tesis. Con ellas se planteó tanto contribuir al conocimiento ecológico básico de una especie arbórea de amplia distribución en nuestro país, como aportar bases sólidas para la recuperación de la misma en las condiciones específicas de los sitios perturbados del Ajusco Medio, D. F. y zonas similares. Debido a que la zona metropolitana de la ciudad de México constituye uno de los sitios con mayor densidad poblacional del mundo y las zonas naturales que la rodean presentan un fuerte deterioro ambiental, se espera que el conocimiento generado por estas investigaciones sea una aportación importante para la rehabilitación de los encinares dominados por esta especie o para su reintroducción en los sitios en que antes se presentó este tipo de vegetación.

El primer artículo analiza el efecto que tiene la variación del tamaño de la semilla en el desempeño de las plántulas de dos especies de encinos, tanto en condiciones óptimas como en presencia de herbivoría. Algunos trabajos previos con otras especies de encinos han reportado un efecto del tamaño de las semillas en la talla inicial de las plántulas (*Quercus montana*, McComb 1934; *Quercus douglasii*, Tecklin y McCreary 1991), y en la germinación, crecimiento y supervivencia de plántulas en condiciones naturales (*Quercus dealbata* y *Q. griffithii*, Triphati y Khan 1990). En este caso, además de analizar si se presentaba esta relación entre tamaño de semillas y de plántulas en dos especies mexicanas, se buscó: a) poner a prueba la hipótesis de que los encinos blancos (subgénero Leucobalanus) presentan una rápida germinación y transporte de

reservas de los cotiledones a las plántulas como un medio de escapar al consumo de bellotas post-dispersión que realizan algunos depredadores, principalmente roedores, y establecer si el éxito en el "escape" está relacionado con el tamaño de la semilla, y b) probar si el disponer de una cantidad variable de nutrimentos (en función de la presencia de cotiledones y el tamaño de la semilla) producía una respuesta diferencial, en términos de supervivencia y/o crecimiento posterior, en caso de una pérdida importante de biomasa aérea.

Los resultados obtenidos nos llevaron a constatar que el encino blanco (*Q. rugosa*) presentó una mayor supervivencia a la pérdida temprana de los cotiledones en relación al encino rojo (*Q. laurina*), el cual parece mantener una dependencia más prolongada con las reservas contenidas en su semilla. En ambas especies el tamaño de semilla afectó la supervivencia. La capacidad de sobrevivir a la pérdida de los cotiledones está mediada por el tamaño de la semilla en *Quercus rugosa*, debido a que las plántulas provenientes de semillas grandes sobreviven en mayor proporción que las provenientes de semillas pequeñas, lo que está relacionado con un mayor desarrollo radicular de las primeras, probablemente debido a una mayor translocación de nutrimentos de la semilla a la raíz. De manera similar, la pérdida de biomasa aérea (herbivoría) redujo más drásticamente la supervivencia de plántulas provenientes de semillas chicas que la de aquéllas originadas de semillas grandes.

La talla y biomasa final de las plántulas de esta especie también se vio afectada por el tamaño de la semilla, la presencia o ausencia de los cotiledones, y la herbivoría. La capacidad de las semillas de crecer en respuesta a la pérdida de biomasa aérea se correlacionó positivamente con el tamaño de la semilla, tanto en presencia como en

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ausencia de cotiledones y dado que estos tuvieron un efecto significativo en las tasas de crecimiento relativo (RGR), se comprobó que las reservas remanentes en los cotiledones un mes después de la germinación aún son importantes para las plántulas, sobre todo en caso de herbivoría, siendo comparativamente menos importantes para las plántulas provenientes de semillas grandes. Estos resultados refuerzan la conclusión de que estas últimas alcanzan una mayor independencia relativa de los cotiledones un mes después de la germinación. En el caso de *Q. laurina*, se comprobó el efecto del tamaño de la semilla en la talla y biomasa final de las plántulas, pero esta variable no afectó las tasas de crecimiento relativo (RGR) que se presentaron en respuesta a la herbivoría.

En resumen, de este trabajo puede concluirse que: a) el tamaño de la semilla influye significativamente en la supervivencia y en la biomasa final de las plántulas de ambas especies; b) ambas especies dependen de las reservas contenidas en sus cotiledones un mes después de la germinación, pero la dependencia es más marcada en el encino rojo (*Q. laurina*) que en el encino blanco (*Q. rugosa*); c) el tamaño de la semilla influye en la capacidad de sobrevivir a la pérdida de cotiledones y a la herbivoría en *Q. rugosa*; d) la presencia de cotiledones y el tamaño de la semilla influyen en el crecimiento posterior a la pérdida de biomasa aérea en esta especie y, e) las plántulas de ambas especies no pueden reponerse totalmente a una pérdida importante de biomasa aérea (herbivoría) en una temporada de crecimiento.

En el segundo artículo se analizan con cierto detalle los factores del medio físico y biológico que influyen en la capacidad de las plántulas de *Q. rugosa* para establecerse y sobrevivir en distintos ambientes, que corresponden a los tres principales tipos de parches que se encuentran en la zona de estudio. Este trabajo mostró que:

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- existe un consumo importante de bellotas por roedores, los cuales localizan más rápidamente los cúmulos con una alta densidad que las semillas solitarias o en grupos pequeños, y que la remoción de semillas difiere entre los sitios, con una mayor tasa de remoción en el borde del bosque que en el matorral perturbado. Sin embargo, una proporción variable de semillas escapa a la depredación por un periodo suficiente para que se produzca la germinación, dadas las condiciones adecuadas.

- las probabilidades de germinación de semillas y establecimiento de plántulas son bajas en el sitio perturbado debido a que están expuestas a una rápida desecación y a la dureza del sustrato, mientras que en el borde o el interior del bosque son mayores (15-20%).

- las principales causas de mortalidad de las plántulas difieren entre sitios. En el sitio perturbado destaca la falta de humedad durante la temporada de secas, mientras que en el interior del bosque el ataque de hongos y la herbivoría son más importantes. En el borde del bosque se da la mayor supervivencia en condiciones climáticas "medias", pero en caso de una temporada de secas extremosa la mortalidad por desecación se incrementa. En este último caso se hacen evidentes las diferencias entre los distintos microambientes de la zona de borde, ya que las plántulas registran una mayor supervivencia en micrositios parcialmente sombreados en comparación con la que se presenta en los micrositios abiertos o totalmente sombreados.

- en el sitio con mayor supervivencia (i.e. el borde de bosque) se mostró una correlación positiva entre tamaño de la semilla y supervivencia de las plántulas.

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- el crecimiento de las plántulas difiere entre sitios: es muy limitado en el interior del bosque, lo que se relaciona con la baja disponibilidad de luz, mientras que en el sitio perturbado es marcadamente estacional, con disminuciones en el área foliar y la altura causadas por la muerte de la parte apical durante la temporada de secas. Las plántulas intactas (i.e. que no sufrieron herbivoría y/o muerte de la parte apical) del borde del bosque y el sitio perturbado presentaron una altura similar, pero el mayor diámetro basal y área foliar de estas últimas sugiere que el crecimiento se incrementa en condiciones abiertas de alta luminosidad.

Los resultados de esta investigación, además de aportar conocimientos sobre el nicho de regeneración de esta especie, permiten hacer algunas recomendaciones prácticas para su manejo en la zona. En primer lugar, la alta depredación de semillas y el frecuente secado (o pudrición, según sea el caso) de las bellotas hacen poco adecuado el esparcirlas o sembrarlas como técnica para reintroducir encinos en la zona. Por otro lado, dada la estrecha relación que existe entre micrositio y supervivencia de plántulas, y la alta mortalidad presente en los sitios perturbados, su trasplante masivo tendrá muy poco impacto, por lo que es más apropiado el trasplante selectivo a micrositios específicos, cuidadosamente seleccionados, que imiten las condiciones de sombra parcial y aporte de hojarasca al suelo que se dan en el borde del bosque. De ser posible, la protección de plántulas mediante cilindros de malla o tubos que eviten el acceso a los herbívoros y proporcionen sombra durante la temporada de secas sería muy recomendable, ya que les permitiría alcanzar más rápidamente una talla en la cual son menos susceptibles tanto a la acción de los herbívoros como a la sequía estacional.

El tercer trabajo aborda el estudio de la dinámica poblacional de Q. rugosa. El análisis demográfico mostró que, en las condiciones actuales, la población se encuentra estable. Este limitado crecimiento poblacional puede deberse tanto a las características propias de la especie (muchas especies de encinos registran problemas de regeneración y tasas de crecimiento individual muy lentas, Ovington y Mac Rae 1960, Shaw 1968, Griffin 1070, Thadani y Ashton 1995), como a las condiciones del sitio. Actualmente la regeneración y por lo tanto el crecimiento poblacional se produce en la zona de transición entre el bosque y el matorral, y el avance del encinar sobre el sustrato basáltico del matorral puede considerarse como una parte importante de un proceso sucesional que es de por si lento. Tomando en cuenta las limitaciones que esto impone para la reintroducción de Q. rugosa en el matorral perturbado, se exploró, usando simulaciones realizadas mediante la modificación de las entradas de la matriz de proyección poblacional, el impacto que tendría la aplicación de distintas técnicas encaminadas a favorecer el crecimiento poblacional.

La primera técnica considerada fue la de realizar aclareos, o eliminación de ramas de árboles y arbustos, que permitieran liberar el crecimiento de individuos supresos de las categorías de brinzales (saplings) y juveniles. Se analizó tanto el impacto que tendría el aplicar este aclareo a cada una de estas categorías por separado como a las tres categorías pre-reproductivas en conjunto, y en cada caso se consideró el resultado de liberar ya fuera a 1/3 o a 1/2 de los individuos supresos en cada categoría. Los resultados mostraron que esta práctica tiene un impacto limitado cuando se dirige a una sola categoría de tamaño, pues no se logra alcanzar un crecimiento poblacional del 1% anual, mientras que si se libera simultáneamente a la mitad de los individuos

supresos de las tres categorías consideradas, se puede lograr un crecimiento cercano al 2%, lo que representa un incremento en relación al valor original de λ.

La segunda técnica analizada fue la introducción artificial de plántulas, de tal forma que se incremente el ingreso de individuos a la población. Esta es una práctica usual que implica producir plántulas en vivero y trasplantarlas, y de tomarse en cuenta los resultados obtenidos en el estudio anterior, éstas podrían ser colocadas en micrositios adecuados, conducentes a una alta supervivencia y un buen crecimiento, garantizando así un reclutamiento real de individuos a la población.

El impacto que tendría en λ el duplicar la entrada de plántulas a la población (respecto a los valores encontrados en condiciones naturales) es similar al que producido por el aclareo de 1/3 de los individuos en las categorías de brinzales y juveniles (saplings, juveniles 1 y juveniles 2), mientras que si se triplica la entrada de plántulas se produce un resultado similar al obtenido mediante la liberación de ½ de los individuos en estas mismas categorías. Finalmente, en la búsqueda de un mayor incremento en el crecimiento poblacional, ambas técnicas se pueden combinar, y bajo este escenario se obtienen los mejores resultados, con un crecimiento poblacional cercano al 4% anual.

Aunque el análisis de elasticidad mostró que los valores más altos de elasticidad se asocian a la permanencia de los adultos, el plantearse incrementar los valores de permanencia y de transición de estas categorías en la matriz de proyección original resulta poco realista. En el caso de los árboles adultos, por tanto, resulta más útil explorar el impacto que tendría una tasa mayor de mortalidad a la registrada en

condiciones naturales. Por el contrario, el análisis del impacto en el crecimiento poblacional de las distintas técnicas de manejo ensayadas en las categorías pre-reproductivas mostró ser una herramienta útil en la elaboración de una estrategia orientada a favorecer la expansión de Q. *rugosa* en el matorral perturbado.