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Acorn removal, seedling survivorship, and seedling growth of *Quercus crispipilis* in successional forests of the highlands of Chiapas, Mexico¹

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ABSTRACT

QUINTANA-ASCENCIO, P. F., M. GONZÁLEZ-ESPINOSA AND N. RAMÍREZ-MARCIAL (Centro de Investigaciones Ecológicas del Sureste, Apartado Postal 63, San Cristóbal de Las Casas, Chiapas, 29200, México). Acorn removal, seedling survivorship, and seedling growth of *Quercus crispipilis* in successional forests of the highlands of Chiapas, Mexico. Bull. Torrey Bot. Club 119: 6–18, 1992.—*Quercus crispipilis* (Trel.) is a dominant tree in mature pine-oak forests of the highlands of Chiapas (Mexico) and Guatemala. Seedlings and saplings of oaks and pines are found in early, open, seral communities, but are infrequent under the closed canopy of dense stands. To better define some of the factors affecting the regeneration of *Q. crispipilis* in fragmented forests, we studied acorn removal by animals, and the survival and growth of transplanted seedlings (2 months old) and saplings (30 months old) during a 21-month period in five seral stands (Grassland, Shrubland, and Early Successional, Mid-Successional, and Mature Forest). Seed removal was high in all stands during April–July 1988, but it was lower in non-forested sites when acorns were abundant on the ground (October and November). Survival of seedlings was low in forested stands with deep shade, and mortality was frequently associated with damping-off. Leaf number per seedling increased with time in the open sites, and did not significantly change in the more open forest areas. Survival of saplings in the grassy stand was lower than in the other sites, and sheep browsing and trampling were the main causes of their death. The highest survival and number of leaves were recorded for saplings at the shrubby stand. It is concluded that *Q. crispipilis* is not able to regenerate under deep shade, but requires open patches in which browsing and trampling by ungulates is absent or minimal. Habitat fragmentation caused by traditional land use patterns in the study area does not seem to hinder, and may even facilitate, the natural regeneration of tropical highland pine-oak forests.

Key words: *Quercus crispipilis*, seed removal, seedling survivorship, succession, montane cloud forest, tropical highlands, Central America, Mexico.

Regeneration of dominant tree species in forest habitats is frequently associated with the removal of suppression or the release of resources resulting from disturbance (Brokaw 1985; Runkle 1985). Differences among species in their micro-

habitat requirements for regeneration have been used to rank species along a continuum of “shade tolerance” (Augspurger 1984a; Collins and Good 1987), and may be relatively well known for some taxa (e.g., *Quercus rubra*; Crow 1988). The regeneration of tree species may also be affected by seed predators (Watt 1919; Shaw 1968a, 1968b; Barnett 1977; Darley-Hill and Johnson 1981; Boucher 1982; Sork *et al.* 1983; Sork 1984), pathogens (Augspurger and Kelly 1984; Hilton *et al.* 1987), herbivores (Dunn *et al.* 1987; Tsiouvaras 1988), competitors, and/or mutualists (Goldberg 1982, 1985; DeGange *et al.* 1989). Most of these studies on regeneration have been conducted in well preserved, homogeneous habitats, or in small natural gaps in the forest. The effect of these factors in heterogeneous habitats, such as those caused by forest fragmentation, may be different (Janzen 1985, 1986; Lovejoy *et*

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al. 1983, 1986; Wilcove *et al.* 1986; Gibson *et al.* 1988; Borchert *et al.* 1989).

Oak and pine-oak forests are common to the subhumid and cool mountainous regions (1300–2500 m) of southern Mexico and Central America (Miranda 1952; Miranda and Hernández-Xolocotzi 1963; Rzedowski 1978; Breedlove 1973, 1981; Jiménez *et al.* 1988). In the highlands of Chiapas (Mexico) and Guatemala it is possible to find some of the better developed stands of this type of forest (Standley and Steyermark 1952; Miranda and Hernández-Xolocotzi 1963). Since pre-Columbian times extensive areas of these forests have been cleared for shifting cultivation of annual crops and logged for fuelwood and charcoal burning (Collier 1975; Veblen 1978; Alemán-Santillán 1989). Current slash-and-burn agriculture on steep slopes, together with sheep grazing and commercial logging, maintains a landscape with a complex mosaic of successional communities (Wagner 1962).

The upper canopy of mature forests is frequently dominated by a relatively few oak and pine species. These trees seem to regenerate best in open stands, with saplings being infrequent (even though seedlings may be seasonally abundant) in the understory of mature stands. The purpose of our study was to compare acorn, seedling (2–23 months old), and sapling (30–51 months old) survivorships of Chiquinib oak (*Quercus crispipilis* Trel.) in five seral communities (Grassland, Shrubland, Early Secondary Forest, Mid-Successional Forest, and Mature Forest) associated with the traditional land use patterns in the highlands of Chiapas.

Materials and Methods. The study was conducted in two sites located at Huixtán (16°45'N, 92°30'W), in the middle of the highlands of Chiapas, Mexico, at an elevation of 2350–2400 m. The regional climate is temperate subhumid (García 1987), with 14–15°C mean annual temperature (nocturnal freezing temperatures are frequent in non-forested areas from December through March), and with 1100–1200 mm annual rainfall (more than 80% of the rainfall occurs from May through October; data from 15-year records at the Chilil weather station, and from 50-year records at San Cristóbal de Las Casas). The soils are dark brown, clayey loams, moderately deep (30–50 cm), and derived from calcareous rocks. The vegetation includes patches of diverse secondary communities associated with pine-oak forests, and on the highest peaks, with montane cloud forest (Miranda 1952;

Breedlove 1981). A more detailed account of vegetation at the study sites appears in Quintana-Ascencio (1989) and González-Espinosa *et al.* (1991).

We identified the following adjacent seral communities (all in Ejido Chilil, except for Mature Forest, which was found in Rancho Merced-Bazom; Table 1):

- (a) Grassland: with sporadic grazing by sheep; this stage remains as a disclimax if moderately grazed.
- (b) Shrubland: with sporadic sheep grazing and dominance by the shrub *Baccharis vaccinioides* H.B.K. and the fern *Pteridium aquilinum* L.
- (c) Early Secondary Forest: 20–25 yr old; 80–90% canopy cover, with *Myrica cerifera* L., *Rhamnus* sp., and non-reproductive (10–15 m height) individuals of *Pinus* spp., *Quercus laurina* Humb. & Bonpl., *Q. rugosa* Nee, and *Q. crassifolia* Humb. & Bonpl. in the canopy.
- (d) Mid-Successional Forest: 40–45 yr old; 70–80% canopy cover, with reproductive individuals of *Q. laurina*, *Q. crassifolia*, *Q. rugosa*, *Pinus oocarpa* Schiede, *P. pseudostrobus* Schlecht, and *P. oaxacana* Mirov in the canopy (20–25 m height), and *Rapanea juergensenii* Mez, *Symplocos limoncillo* Humb. & Bonpl., *Oreopanax xalapensis* (H.B.K.) Decne. & Planch., *Fuchsia microphylla* H.B.K., *F. thymifolia* H.B.K., and *Litsea glaucescens* H.B.K. in the understory.
- (e) Mature Forest: 80–100 yr old; tallest trees reach 35–45 m. Canopy dominants are *Q. laurina*, *Q. crassifolia*, and to a lesser extent *P. oocarpa* and *P. oaxacana*. A treelet stratum (5–15 m) is mostly dominated by *Rapanea juergensenii* and *Oreopanax xalapensis*, but it also includes *Cleyera theaeoides* (Sw.) Choisy, *Ternstroemia pringlei* (Rose) Standl., *Symplocos limoncillo*, *Persea* sp., *Magnolia sharpii* Miranda, and arborescent ferns (Cyatheaceae). A dense and diversified shrub stratum (1–3 m) includes *Miconia* aff. *hemenostigma* Naud., *Fuchsia splendens* Zucc., *F. paniculata* Lindl., *F. thymifolia*, *F. microphylla*, *Viburnum jucundum* Morton, *Saurauia oreophilla* Hemsl., *S. latipetala* Hemsl., *Cestrum anagyris* Dunal, *Verbesina* sp., and many ferns such as *Woodwardia spinulosa* Mart. & Gal., *Polypodium* spp., *Thelypteris* spp., and *Lophosoria quadripinnata* (Gmel.) C. Chr.

SPECIES. *Quercus crispipilis* is an evergreen tree

Table 1. Vegetation structure of the study stands. More detailed information in González-Espinosa *et al.* (1991).

Community strata ^a	Density (ind/m ²)	Cover (cm ² /m ²)	Canopy cover (%)
Grassland (GR)			0.0
Herbs	—	82 ^b	
Shrubland (SH)			0.27 ± 0.23
Herbs	—	60 ^b	
Shrubs	1.64	280	
Early Successional Forest (EF)			0.83 ± 0.14
Herbs	25.60	1197	
Shrubs	1.65	5405	
Trees ^c	0.85	6.4 ^d	
Mid-Successional Forest (MF)			0.76 ± 0.11
Herbs	42.43	2748	
Shrubs	1.30	4001	
Low trees	0.17	1.1 ^d	
Canopy trees	0.11	3.0 ^d	
Mature Forest (MA)			0.94 ± 0.03
Herbs	35.50	451	
Shrubs	3.54	11,517	
Low trees	0.38	1.5 ^d	
Canopy trees	0.06	2.5 ^d	

^a Herbs (<0.5 m height): point-intercept method (in GR and SH), or quadrats (30 samples, 0.2 × 10.0 m). Shrubs (0.5–3.0 m): quadrat method (25 samples, 2.0 × 10.0 m). Low trees (>3.0 m and <15 cm DBH) and canopy trees (>15 cm DBH): point-centered quarter method (90 points in each stand). Percent canopy cover was obtained with upright photographs (18 in each stand) and 400 points per slide.

^b Percent ground cover; 2000 points/stand.

^c Only one tree layer was considered: 90% of the trees had <15 cm DBH.

^d Sum of the DBH's (cm/m²).

(10–30 m tall), inhabiting dry and rocky slopes in the mountains of Chiapas and Guatemala (1100–2400 m; Standley and Steyermark 1952). *Q. crispipilis* occurs in both of our study areas, but it only becomes dominant below the 2200 m contour line (P. F. Quintana-Ascencio personal observation). Trees with intermediate traits between *Q. crispipilis* and *Q. crassifolia* are frequently found in the study area; these morphs may indicate their introgressive hybridization (D. E. Breedlove personal communication).

ACORN REMOVAL. Acorns were collected in March–November, 1988, at Rancho Nuevo, San Cristóbal de Las Casas, Chiapas (2200 m), and only those which sank in water (the kind found viable in germination tests) were exposed on the ground to seed predators. From April through November 30 groups (10 acorns each; groups separated by 7–10 m) were exposed each month for a week in each of the five seral stands. All seeds missing after one week were assumed to have been eaten or cached. Each group was marked with a nearby painted nail to allow its relocation. No acorns were available in August and September and acorn predation was not

monitored in these months. The homogeneity of acorn removal among stands was evaluated with G-tests (Zar 1984).

SURVIVORSHIP AND GROWTH OF SEEDLINGS AND SAPLINGS. Acorn seed coats were broken and the seeds were then germinated on damp cotton in the laboratory in April 1988. One-month old seedlings were put in plastic glasses (90 cm³) filled with soil from the study sites, and grown in outdoor conditions. In June 1988 we transplanted 56 seedlings with their root/soil ball to each of the five seral communities (14 four-plant groups separated by 5 m; 1 m between each plant). Height, length of longest leaf, and number of leaves were obtained for each seedling before transplants; plants of similar sizes were selected. In June–November 1988 (monthly), May 1989, and February 1990 we evaluated survivorship, number of old and new leaves, and number of leaves showing insect damage on at least 10% of their area. Cover (length × width), shoot height, and length of largest leaf were recorded in September–November 1988, May 1989, and February 1990. Similar non-destructive variables have been used to detect differences in the per-

Table 2. Probability that a clump of *Q. crispipilis* seeds was found (a), and probability that the clump was completely depleted (b), in each successional stand and month, and G-values obtained with the log-likelihood ratio-test. Data collected during 1988. Stand identification as in Table 1.

Stand	APR	MAY	JUN	JUL	OCT	NOV
(a)						
GR	0.92	1.00	1.00	1.00	0.15	0.92
SH	—	—	1.00	1.00	0.16	0.07
EF	1.00	1.00	1.00	1.00	0.73	0.60
MF	0.55	1.00	1.00	1.00	—	—
MA	0.80	0.93	0.93	1.00	0.90	0.95
G	30.4***	5.6 NS	6.5 NS	0.0 NS	59.1***	64.5***
(b)						
GR	0.73	1.00	1.00	1.00	1.00	0.75
SH	—	—	1.00	1.00	0.03	0.03
EF	0.97	1.00	1.00	1.00	0.20	0.37
MF	0.52	0.97	1.00	1.00	—	—
MA	0.70	0.93	0.93	1.00	0.83	0.95
G	18.1***	4.3 NS	6.5 NS	0.0 NS	71.5***	51.0***

NS = $P > 0.05$, *** = $P < 0.001$.

formance of tree seedlings in contrasting habitats (e.g., Augspurger 1984a). Sample sizes varied as the study progressed due to seedling mortality.

150 saplings (30-months old) grown in black plastic bags (1270 cm³) were obtained from the Campo Experimental Forestal Rancho Nuevo (INIFAP-SARH). Seeds were collected in 1985 in the same forest stands as those for the acorn removal tests in 1988. We measured shoot height and leaf number before transplanting the saplings in June 1988 (30 plants in each stand; 5 m from each other plant). Saplings of similar size were selected for transplants. In July–November 1988, May 1989, and February 1990 we recorded the same variables as for seedlings.

We used Kruskal-Wallis tests (Zar 1984) for the analysis of number of new and total leaves. The Wilcoxon matched-pairs test (statistic z or T depending on sample size) was used for the analysis of paired data (Siegel 1956), as those between the initial and final evaluation dates. Log-transformed survivorship data were compared by testing for equal slopes of regression lines (Zar 1984). Homogeneity of insect damage on leaves among seral conditions was evaluated with G-tests (Zar 1984). In all cases n means sample size.

RODENT TRAPPING. In May, August, and November 1988, we set 60 Tomahawk traps (25.0 × 7.0 × 7.5 cm) on two consecutive nights in each forested successional condition (120 trap-nights/stand). The traps were baited with rolled oats and set on an imaginary grid 7–8 m from each other. Every captured rodent was ear-marked with paint and released.

Results. Rodent trapping and bird watching (identification was based on Hall and Kelson 1959; Alvarez del Toro 1964) from May–November 1988 indicated that the main predators of acorns on the ground at the study site were Brush Mouse (*Peromyscus boylii levipes* Merriam), Chiapan Deer Mouse (*P. zarhynchus* Merriam), Fulvous Harvest Mouse (*Reithrodontomys fulvescens chiapensis* A. H. Howell), Guatemalan Gray Squirrel (*Sciurus griseoflavus chiapensis* Nelson), Band-tailed Pigeon (*Columba fasciata fasciata* Say), Black Throated Jay (*Cyanolyca pumilo pumilo* Strickland), and Steller's Jay (*Cyanocitta stelleri ridgwayi* Miller & Griscom). The probability that at least one acorn could be removed from any given clump (roughly equivalent to the probability that the clump could be found by seed predators; González-Espinosa 1982; Price and Jenkins 1986) differed among the successional stands, except during the summer months when almost all clumps were found and completely depleted (Table 2). Variation among months was lowest in Mature Forest and highest in Shrubland. In general, however, seed predators were adept at locating the seeds.

SEEDLINGS. The survivorship of seedlings from June 1988 to February 1990 varied among seral conditions (Fig. 1a). Mortality was significantly higher in the densest stands (crown cover > 80%; over 25,000 shrubs and trees per ha), and was mostly due to damping-off. All seedlings transplanted in the Early Successional and Mature Forest stands were dead after 21 months. However, 30–40% of seedlings in the other stands survived.

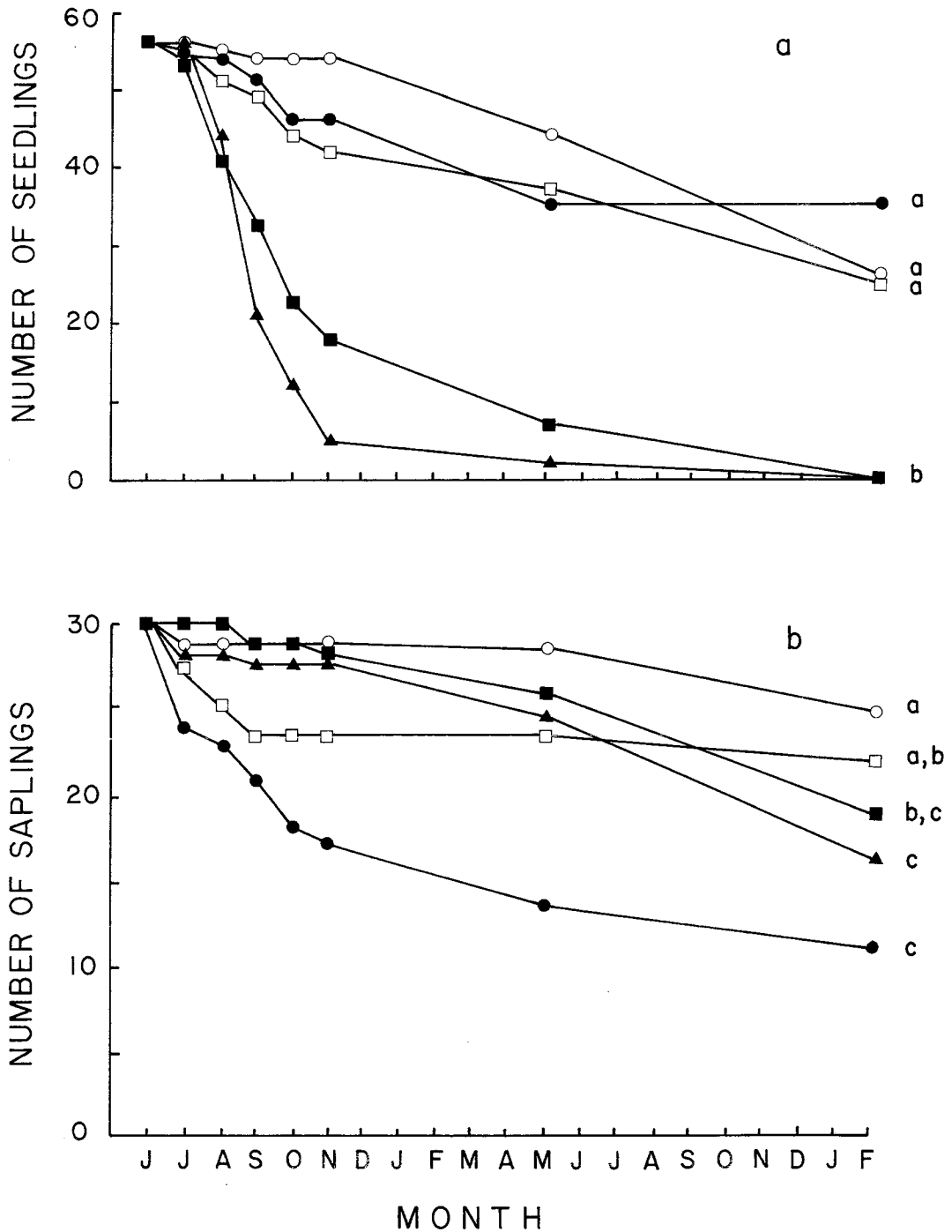


Fig. 1. Survivorship of *Q. crispipilis* seedlings (a) and saplings (b) during 21 months in five successional stands (● = Grassland; □ = Shrubland; ■ = Early Successional Forest; ○ = Mid-Successional Forest; ▲ = Mature Forest). Mid-Successional Forest data from October 1988 through February 1990 were proportionally calculated (based on 28 instead of 30 for saplings, and 48 instead of 56 for seedlings) due to disturbance by selective logging. Significant differences ($P < 0.05$) among the slopes of the regressions (with log transformed data; Zar 1984) are indicated with different letters.

Table 3. Results of Kruskal-Wallis tests for leaf number (TL) and number of new leaves (NL) of *Q. crispipilis* seedlings and saplings.

Month	Seedlings		Saplings	
	TL	NL	TL	NL
JUN 88	4.28 NS		2.82 NS	
JUL 88	4.17 NS		13.80*	74.44***
AUG 88	28.50***	31.43***	4.76 NS	39.70***
SEP 88	61.56***	40.11***	11.19*	34.67***
OCT 88	42.91***	22.63***	8.55 NS	13.13*
NOV 88	40.70***	11.41*	22.10***	5.07 NS
MAY 89	21.59***	37.69***	28.42***	55.20***
FEB 90	17.78***	4.35 NS	33.05***	6.03 NS

NS = $P > 0.05$, * = $P < 0.05$, *** = $P < 0.001$.

The number of leaves varied among successional stands from two months after having been transplanted to the field (Fig. 2, Table 3). From June 1988 to February 1990, there were increases in mean leaf number in seedlings planted in Grassland (Wilcoxon's test: $z = -4.5$; $N = 35$, where N is the number of matched pairs minus the number of pairs with difference equal to zero; $n = 36$, $P < 0.001$; Siegel 1956) and Shrubland ($T = 8$, $N = 23$, $n = 25$, $P < 0.001$). There were no significant differences ($P > 0.05$) for seedlings in Mid-Successional Forest ($T = 99$, $N = 21$, $n = 26$). All seedlings in the Mature and Early Successional Forest stands had died by February 1990. From August 1988 onwards, the number of new leaves was significantly different among seral conditions (Fig. 2, Table 3). Those seedlings transplanted to Grassland generally produced more leaves than those in the other stands, and by May 1989 had replaced 90% of their leaves.

From August 1988 up to February 1990 the height of surviving seedlings changed significantly in Grassland, Shrubland, and Mid-Suc-

cessional Forest (Table 4). Seedling cover and the length of the longest leaf varied between September 1988 and February 1990 in the Shrubland and Mid-Successional Forest stands (Table 4). The mean length of the longest leaf did not differ throughout the period of the study in any of the successional conditions (Table 4).

Herbivore damage on seedlings (10–20% of leaf area on <25% of each individual's total leaves) was not different among seral stands.

SAPLINGS. The survivorship of saplings differed among successional conditions at the end of the period of study (Fig. 1b). Mortality of saplings in Grassland and Shrubland was caused by sheep browsing and trampling. Dead saplings in the forested stands wilted without any apparent mechanical damage, but showed some pathogen attack.

A general, but not uniform, decreasing trend for mean leaf number of saplings occurred in all seral conditions (Fig. 3). By February 1990 saplings in Shrubland had significantly ($P < 0.001$)

Table 4. Mean (\pm one standard error) height, cover and length of the longest leaf of *Q. crispipilis* seedlings, and T or z values from Wilcoxon's tests for the differences between initial and final data for the same variables (n = number of matched pairs with sign). Stand identification as in Table 1.

Stand	n	Height (cm)			Cover (cm ²)			Length of longest leaf (cm)		
		AUG 88	FEB 90	T or z	SEP 88	FEB 90	T or z	SEP 88	FEB 90	T or z
GR	36	4.0 (0.15)	7.4 (0.81)	3.3*** N = 34	3.5 (0.27)	4.7 (0.71)	1.1 NS N = 36	3.0 (0.15)	3.6 (0.22)	1.5 NS N = 28
SH	25	4.3 (0.20)	10.2 (1.09)	4.0*** N = 25	3.2 (0.27)	4.7 (0.72)	87.0* N = 25	3.8 (0.27)	3.7 (0.72)	111.0 NS N = 21
EF		4.1 (0.20)	—	—	3.6 (0.34)	—	—	4.4 (0.09)	—	—
MF	25	4.7 (0.28)	10.7 (0.77)	3.0*** N = 25	6.4 (0.28)	4.0 (0.44)	3.9*** N = 26	4.8 (0.10)	4.4 (0.27)	102.0 NS N = 23
MA		4.3 (0.20)	—	—	3.3 (0.57)	—	—	4.3 (0.19)	—	—

NS = $P > 0.05$, * = $P < 0.05$, *** = $P < 0.001$.

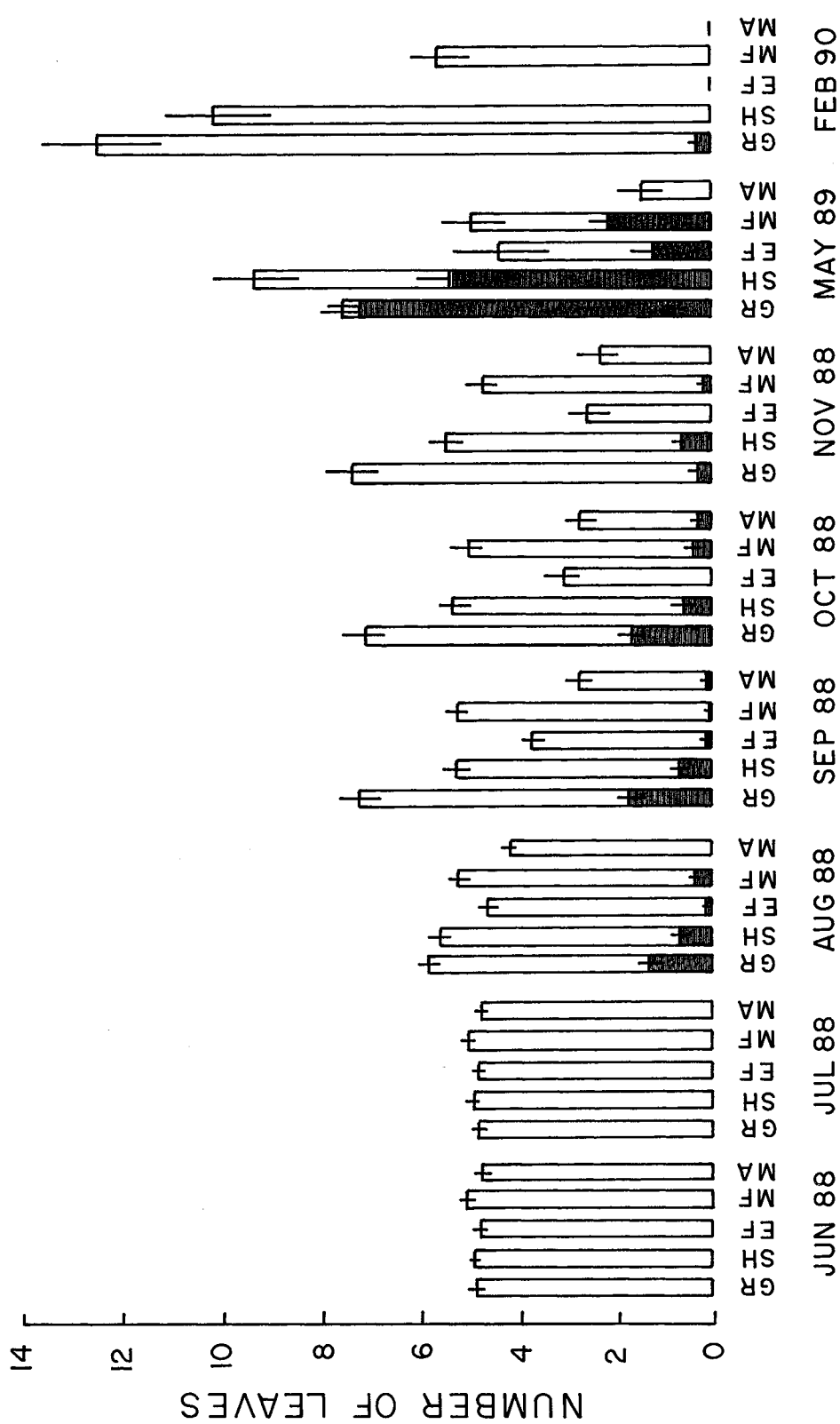


Fig. 2. Total leaf number (whole bars; mean \pm one standard error) and number of new leaves (shaded portion of bars; mean \pm one standard error) of *Q. crispipilis* seedlings at the end of 21 months of study in the five successional stands. See Table 1 for stand identification.

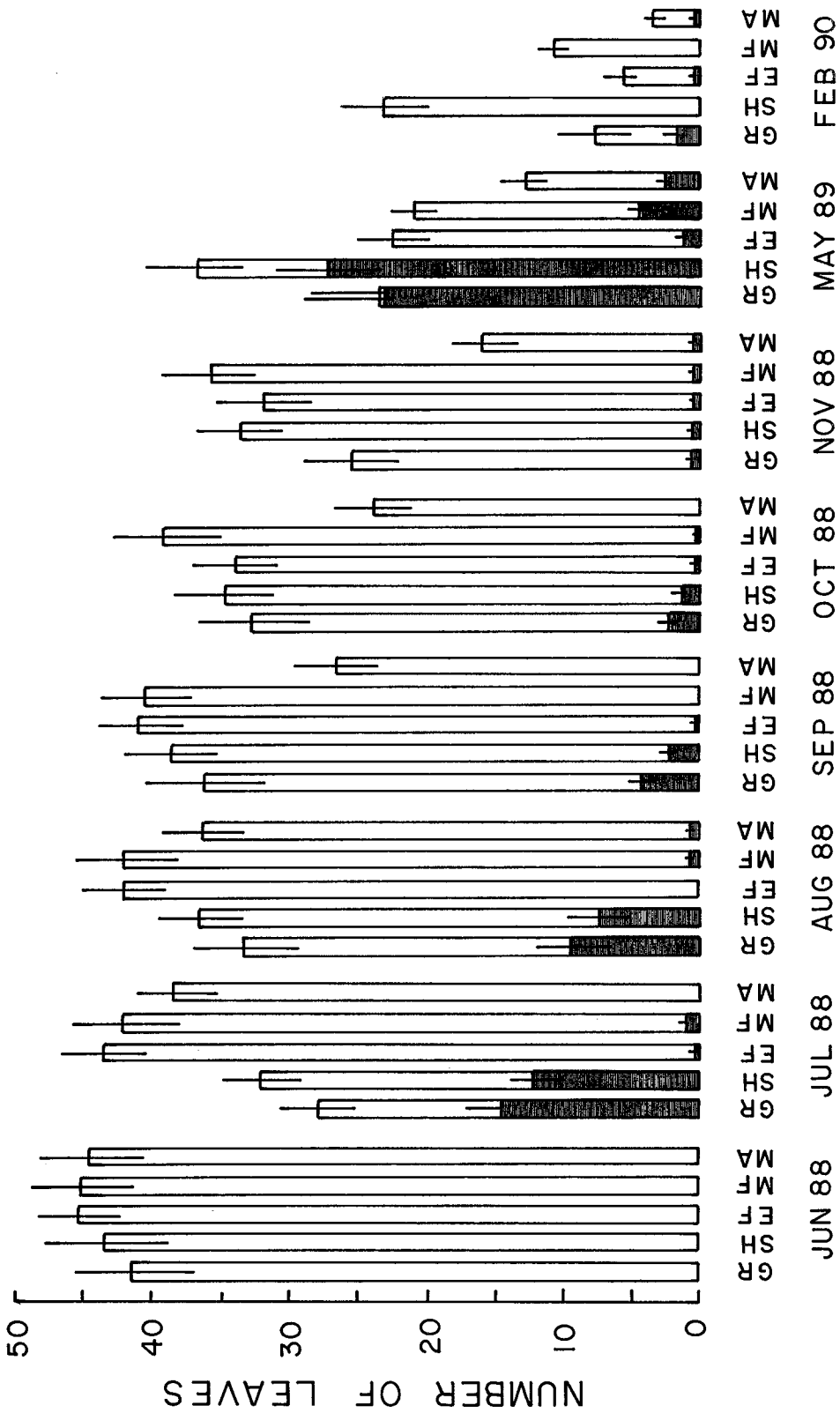


Fig. 3. Same as Fig. 2, but for *Q. crispipilis* saplings.

Table 5. Mean (\pm one standard error) height, cover, and length of the longest leaf of *Q. crispipilis* saplings, and T or z values from Wilcoxon's tests for the differences between initial and final values for the same variables (n = number of matched pairs with sign). Stand identification as in Table 1.

Stand	n	Height (cm)			Cover (cm ²)			Length of longest leaf (cm)		
		MAY 88	FEB 90	T or z	SEP 88	FEB 90	T or z	SEP 88	FEB 90	T or z
GR	11	14.7 (0.56)	12.5 (2.41)	11.0 NS N = 11	14.2 (1.83)	12.9 (5.09)	28.0 NS N = 11	5.6 (0.30)	3.8 (0.78)	9.0 NS N = 9
SH	22	13.1 (0.79)	13.3 (0.84)	88.5 NS N = 19	17.8 (2.07)	21.3 (2.93)	82.0 NS N = 22	5.6 (0.26)	5.4 (0.36)	96.0 NS N = 20
EF	19	14.2 (0.52)	19.2 (0.89)	2.0*** N = 15	25.3 (1.56)	14.5 (2.54)	20.0** N = 19	6.2 (0.16)	7.5 (0.53)	35.5* N = 18
MF	25	13.4 (0.56)	18.0 (1.53)	32.0*** N = 25	28.3 (1.73)	22.4 (2.96)	99.5 NS N = 25	6.5 (0.20)	7.7 (0.46)	81.5 NS N = 24
MA	16	13.3 (0.56)	16.8 (1.42)	25.0 NS N = 15	20.6 (1.64)	8.2 (1.93)	1.0*** N = 16	5.9 (0.18)	6.1 (0.51)	46.5 NS N = 14

NS = $P > 0.05$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

more leaves than those in Grassland, Early Successional and Mature Forests; Mid-Successional Forest was intermediate (Fig. 3, Table 3). Browsing damage by sheep from May through July 1988 decreased the number of leaves of saplings in Grassland and Shrubland (Fig. 3). However, those plants which lost more leaves produced a higher number of new leaves ($r = 0.39$, $n = 50$, $P < 0.01$; Fig. 4).

Saplings in the Early Successional and the Mid-Successional Forest stands showed significant mean height changes from May 1988 through February 1990 (Table 5). No changes in height were observed during the same period in Mature Forest, Shrubland, and Grassland (Table 5).

Cover of saplings decreased from September 1988 up to February 1990 in Early Successional Forest and Mature Forest (Table 5). A significant increase in the length of the largest leaf was only recorded in the Early Successional Forest (Table 5). In general, the lowest values for both variables were recorded in Grassland, Shrubland and Mature Forest and the highest in Mid-Successional Forest.

Herbivore insect damage on saplings (10–20% of leaf area on <30% of each individual's total leaves) was not different among successional conditions.

Discussion. Traditional land use patterns in the highlands of Chiapas are similar to those occurring elsewhere in populated tropical highland areas. Under less intensive land use, shifting agriculture in forested regions resulted in a heterogeneous landscape with seral stands of widely varying successional ages. More recently, this heterogeneity has tended to decrease as more ex-

tensive areas are permanently used as grazing lands. In this study, we have attempted to understand how different fragments of this dynamic landscape affect the recovery and conservation of a dominant species.

Seed removal of *Q. crispipilis* was higher in the forested than in the open stands when acorns were abundant on the ground (October and November). Similar seed removal differences among prairie and deciduous forest sites have been reported by Stapanian and Smith (1986) and Stapanian (1986) with fox squirrels (*Sciurus niger*). On a local scale, populations of seed predators/dispersers may temporarily concentrate on the richest patches of the habitat. González-Espinosa (1982, 1984) induced this response with *Liomys irroratus* (Heteromyidae) when the natural *Opuntia* (Cactaceae) seed and fruit crop was experimentally changed in the field. Differences among habitats in seed removal and dispersal rates have been found to influence the chances of invasion and distribution of tree species in mosaic landscapes. Red squirrels (*Tamiasciurus hudsonicus*) rarely are active far away from trees, thus limiting seed dispersal into open habitats (Benkman *et al.* 1984), but other animals like jays (Bossemma 1979), small rodents (Jensen and Nielsen 1986), and fox squirrels (Stapanian and Smith 1986) may store large seeds in open habitats contributing to their invasion by nut-bearing trees.

The growth and survivorship of seedlings and saplings of *Q. crispipilis* was affected by successional age. The results of transplant experiments show that *Q. crispipilis* grew faster in open sites than in forested stands. However, browsing and trampling by sheep, which typically occurs in

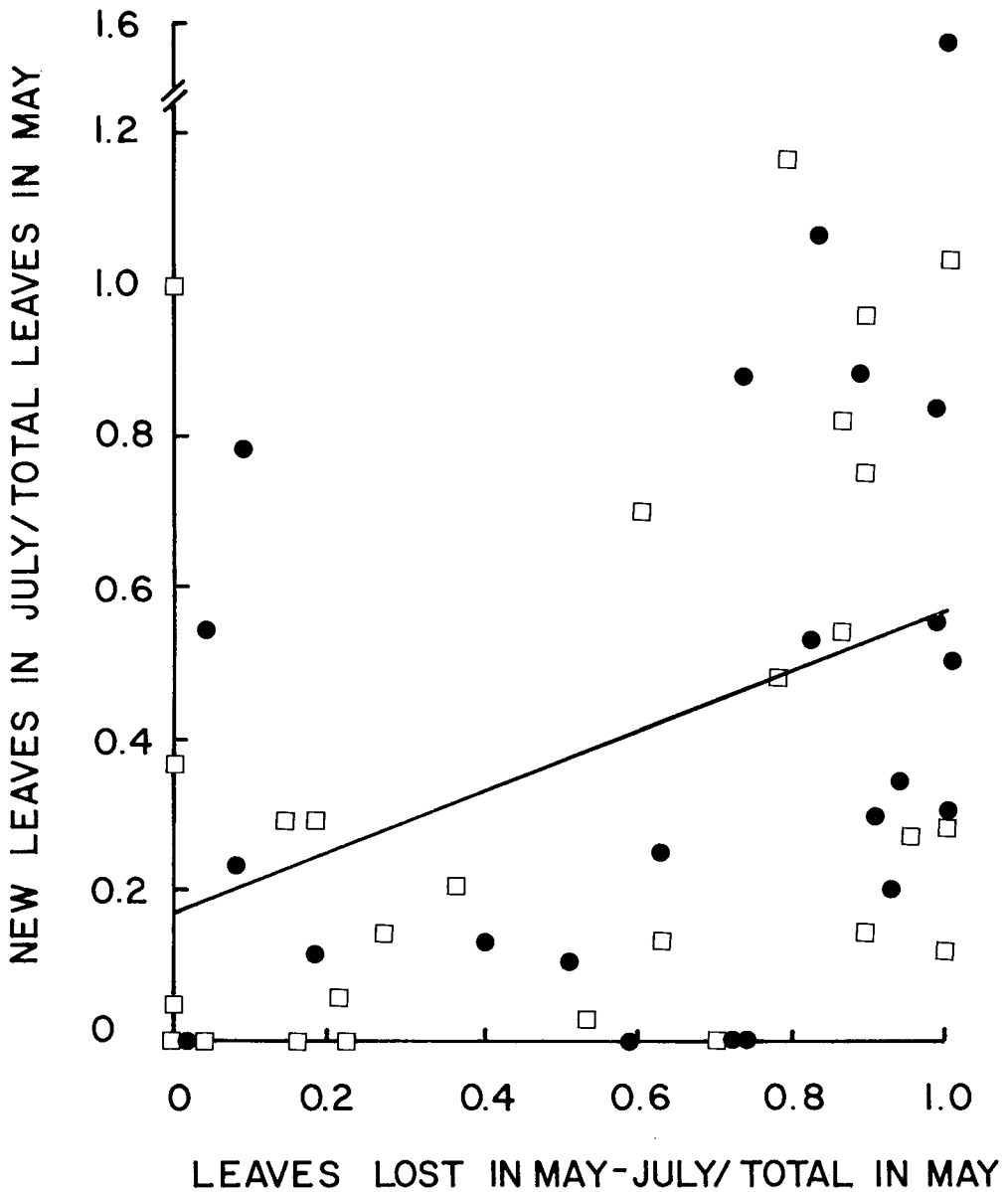


Fig. 4. Relationship between proportion of new leaves produced by *Q. crispipilis* saplings in July 1988 and proportion of leaves lost in May-July 1988 in the Grassland (solid circles) and Shrubland (open squares) stands ($r = 0.39$, $n = 50$, $P < 0.01$).

non-forested habitats under current land cultural practices, was a common cause of plant death and biomass removal in the open stands. Those individuals surviving herbivore damage had the highest leaf turnover rate, as has been previously reported for other *Quercus* species (Hilton *et al.* 1987; Tsiouvaras 1988).

The performance of plants in the Mid-Successional Forest indicates that *Q. crispipilis* can re-

generate under a moderately closed overstory. Under these conditions, by expanding its leaves and elongating its shoot, this oak may adjust leaf temperature and increase light interception and water use efficiency (Parkhurst and Loucks 1972; Givnish 1979). The regeneration of oak species under the rather open canopy of secondary pine forests is common to temperate forests (Quarman and Keever 1962; Auclair and Cottam 1971;

Peet and Christensen 1980, 1987; McCune and Cottam 1985; Takenaka 1986; Crow 1988; Foster 1988).

The low seedling and sapling survivorship and growth observed under very closed canopies (like those of Early Successional and Mature Forests), suggests that this species does not tolerate deep shade; this is corroborated by studies of population dynamics for the other *Quercus* species at our study sites (González-Espinosa *et al.* 1991). The ground-level irradiance regimes in the forested stands could be below the photosynthetic light compensation point of *Q. crispipilis* most of the time. However, no adequate instruments were available to measure these variables in the field, and no information exists about the light requirements of *Q. crispipilis*. Alternatively, and as found elsewhere, the mortality of tree seedlings under shade could be frequently associated with fungal diseases (Vaartraja 1962; Grime 1965; Takenaka 1986). Low light levels under closed canopies decrease temperature and may increase soil and air humidity, creating more favorable conditions for pathogen attack on seedlings (Augspurger 1984b; Augspurger and Kelly 1984). Additionally, litter accumulation in our forested stands could enhance death of seedlings by providing a favorable microhabitat for fungal propagation and growth. Sydes and Grime (1981) found a negative correlation between the biomass of seedlings and herbs and the amount of litter in a *Quercus petraea* forest in Great Britain.

The results indicate that *Q. crispipilis* regeneration may decrease as forest canopy density increases. Forest rejuvenation by small natural and artificial clearings may contribute to *Q. crispipilis* recruitment and the release of its suppression in dense stands. In grassy habitats low acorn availability, and browsing and trampling by sheep, arrest its establishment. Seedlings and saplings in early-successional shrub-dominated communities are more protected against injury by ungulates, and at the same time are exposed to apparently more favorable light, temperature, and humidity conditions for their growth and survivorship.

Tropical highland forests are currently disappearing due to the expansion of grazing areas (Veblen 1978; Jiménez *et al.* 1988; Parra-Vázquez and Mera-Ovando 1989). This trend decreases the complexity of the seral mosaic while increasing the isolation of the remnant late successional forest patches. Our results suggest that the recovery of mountain forests in tropical highlands could be accelerated if early-shrubby and

mid-successional communities are frequent. The conservation of such natural forest resources might, thus, be achieved with the reestablishment of the landscape's heterogeneity and without necessarily preventing agricultural land use. More extensive long-fallow (>25 yr) milpa agriculture and deferred/rotational grazing would provide this heterogeneous landscape.

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NOTES

Scientists Focus on New York's Future in Spring Conference at the New York State Museum

The future of New York State's natural resources will be the focus of scientists from throughout the Northeast, meeting for "The New York Natural History Conference II" at the New York State Museum in Albany April 29 through May 1, 1992.

Keynote speaker is Peter Raven, Director of the Missouri Botanical Garden, one of today's most prominent biologists. Dr. Raven has been concerned with development of the Garden's research programs in tropical and temperate botany. A member of the National Academy of Sciences and a recipient of the International Environmental Leadership Medal, he is author or editor of 16 books and more than 400 scientific papers on topics as diverse as general botany, plant systematics, chromosome biology, biogeography, conservation biology and ethnobotany.

The conference will examine natural history

research in New York State and focus attention on critical research needs.

The program will include presentations by scientists from throughout the Northeast on topics including rare and exotic species, the ecology of lakes and streams, forest and wetland history, animal ecology, the Hudson River and Lake George, and others.

For more information on The New York Natural History Conference call 518/474-5812.

Organization of Biological Field Stations

Summer opportunities for field courses in 1992 offered at biological field stations are summarized in a poster prepared by the Organization of Biological Field Stations. Most offerings are intended for undergraduate and graduate students in biology. For a copy, contact Dr. Richard W. Coles, Secretary OBFS, Washington University Tyson Research Center, P.O. Box 351, Eureka, MO 63025.