New Forests **21:** 59–70, 2001.

Influence of litter on emergence and early growth of *Quercus rugosa*: a laboratory study

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Accepted 5 October 2000

Abstract. Species-rich old-growth forests dominated by *Quercus* were extensive in the highlands of Chiapas until a few decades ago. Current land-use is resulting in replacement of *Quercus* by *Pinus* spp. in the canopy of the remaining forest fragments, which are less diverse, drier, and more exposed to freezing temperatures. Forest floor and soil are also modified and may limit the regeneration of many woody species. We studied the influence of litter type (pine needles vs. oak leaves), litter depth (0, 3, 6 and 14 cm), and litter cover (3 cm vs. 0 cm of loose litter on top of sowed acorns) on the emergence and growth of seedlings of *Quercus rugosa*, a dominant tree in pine-oak forests. Seedling emergence and establishment were affected by the interaction of experimental factors. Uncovered acorns on pine litter were more exposed to desiccation; this effect was more evident with deeper litter. Acorns sowed on oak litter were not affected by levels of litter cover and litter depth. The results can be of use in defining further field studies, and practices of direct seeding for restoration of pine-dominated stands.

Key words: forest floor, germination, pine-oak forest, *Pinus*, seedbed, seedlings

Resumen. Hasta hace pocas décadas prevalencían en Los Altos de Chiapas los bosques con dominancia de *Quercus*. El uso actual del suelo ha ocasionado un reemplazo de *Quercus* por *Pinus* spp. en los rodales remanentes, menos diversos, más secos y más fríos. A su vez, el suelo y el piso forestal han cambiado y pueden limitar la regeneración de muchas especies leñosas. Estudiamos la influencia de atributos del mantillo como el tipo (acículas de pino u hojas de roble), profundidad (0, 3, 6 y 14 cm) y presencia (capa de 3 cm ó nada sobre las bellotas) sobre el establecimiento y crecimiento temprano de *Q. rugosa*, dominante en bosques de pino-encino. La emergencia y establecimiento fueron afectados por la interacción de los factores experimentales. Las bellotas descubiertas sembradas sobre hojarasca de pino estuvieron más expuestas a la desecación, lo cual fue más evidente con mantillo más profundo. Las bellotas sembradas sobre hojarasca de roble no fueron afectadas por el espesor o cubierta de mantillo. Los resultados ayudan para definir subsecuentes estudios de campo y prácticas de restauración en pinares basados en la siembra directa de las bellotas.

Introduction

Natural regeneration of oaks is affected by quantity and quality of acorn production, heavy predation and browsing on acorns and seedlings, and low growth rate of seedlings and saplings (Carvell and Tryon 1961; Shaw 1968; Borchert et al. 1989; Crow 1988). Oak regeneration is low and seedling development poor beneath old-growth stands dominated by oaks or other broadleaved species, mainly due to low light levels, fungal attacks, and acorn predation (Crow 1988; Lorimer et al. 1994). However, conditions under pine-dominated canopies, and in forests edges, may be favorable for regeneration of oaks (Crow 1988; Mosandl and Kleinert 1998; Bonfil and Soberón 1999).

In recent decades, the highlands of Chiapas (1500–2700 m) have undergone a floristic change from forests previously dominated by oaks and other broadleaved species to stands dominated by pines (Ochoa-Gaona and González-Espinosa 2000). This change may be due to: (1) repeated logging of *Quercus* individuals for firewood, even at pre-reproductive sizes, decreasing the number of propagules needed for natural regeneration, and (2) logging of pines mostly after they have attained commercial timber size and produced several seed crops (González-Espinosa et al. 1995). The pinelands include only 20–60% of the number of species of ferns, vines, lianas, shrubs, and understory trees of those occurring in neighboring stands with an oak-dominated canopy (at least 80 years after clearing; González-Espinosa et al. 1995). Similar changes in canopy composition due to human impact or natural disturbances have been documented in other areas where *Pinus*, *Quercus*, and broadleaved species coexist (Richardson and Bond 1991; Schneider 1996). Pine dominance also brings about modifications in the soil and forest floor (Switzer et al. 1979; Klemmedson 1992; Romero-Nájera 2000), that may affect germination and establishment of broadleaved species.

Germination of acorns may be affected by seed burial (Shaw 1968), acorn size (Bonfil 1998), herbaceous cover (Tripathi and Khan 1990), soil moisture (Nyandiga and McPherson 1992), and litter (Barik et al. 1996). Barrett (1931) distinguished litter depth (the layer of litter under the seeds) from litter cover (or “loose litter”), the layer of non-compacted leaves on top of seeds from the last crop, and proposed this latter as a factor determining the fate of acorns. However, the effects of litter cover and type on emergence and growth of oak seedlings are not well understood. As part of a larger study on regeneration of native trees in disturbed forests with varying dominance by *Pinus* spp., we investigated under controlled conditions how litter depth, composition, and cover may influence the emergence and early growth of seedlings of a dominant oak species.

Methods

Species

Quecus rugosa Née (subgenus Leucobalanus: Fagaceae), is a dominant oak (with *Q. laurina* and *Q. crassifolia*) in pine-oak forests from the tropical mountains of Mexico and Guatemala (Nixon 1993). Acorns are produced in September–February, and mast seeding years occur every two years in the study region. Acorns germinate readily after fallen or dispersed by small mammals (rodents and squirrels) and blue jays. Seedling banks occur on the forest floor in March and April. This species resprout vigorously after browsing, lopping, and logging, and its seedlings may occasionally abound in pinelands. Because of its copius seed crops and easy propagation under nursery conditions, *Q. rugosa* has been highly regarded in forest restoration programs (Bonfil and Soberón 1999).

Field and laboratory

In January and February of 1996, acorns were collected from the forest floor of a mature oak forest at Estación Biológica Huitepec, EBH (ca. 30 trees over ca. 10 ha; more site details in Ramírez-Marcial et al. 1998). The acorns were stored for three months at 5 °C in a refrigerator, and only those apparently undamaged (i.e. sinkable in water; Quintana-Ascencio et al. 1992) and relatively large (>2 cm long) were used (Bonfil 1998). The seed coats were lightly broken (without damaging the embryo) to allow hydration of the seed contents for 48 hr before sowing. Samples of forest floor were collected from old-growth oak-dominated forest (at EBH) and pinelands (at Mitzitón, municipality of San Cristóbal de Las Casas). A *machete* was used to cut the samples maintaining vertical layering as intact as possible; the underlying mineral soil (down to 10 cm depth) was also collected. All soil and forest floor materials were sun-dried for 72 hr before placed in perforated plastic trays (24 cm diameter, 16 cm depth) in the laboratory. Additional non-stratified samples of the whole litter (15×15 cm) were collected in the same sites (every 2 m along a 50 m random transect) to estimate litter bulk density. Average bulk densities (pine litter: 0.085 ± 0.024 g/cm^3 and oak litter: 0.081 ± 0.027 g/cm^3) were used to calibrate conditions of experimental seedbeds.

Three factors were studied: litter composition (pine vs. oak), litter depth (0, 3, 6, and 14 cm), and litter cover (seeding acorns with and without a 3 cm cover). The seeds were placed on seedbed layers (identified after Billings 1966) simulating those found in pine- and oak-dominated stands as follows: 2 cm of mineral soil and humus at the bottom (a mixture from all sampled stands), 3 cm of fermentation layer (decomposing litter), 2 cm of broken litter, and on top of these three layers, a layer of variable depth (according to litter depth levels) of recently fallen and intact litter. One-half of the sowed trays were covered with a 3 cm loose cover of pine or oak litter. Each of the 16 factor combinations (30 viable acorns each) was replicated three times.

The experiment was set in a laboratory (May–October) under indoor daylight conditions (33.33 ± 1.32 μm·m^{-2}·seg^{-1}), similar to those found under broadleaved trees in the forest (Ramírez-Marcial et al. 1998). Sunlight movements during the day exposed all trays to direct light at least 1–3 hours daily (up to 1700 μm·m^{-2}·seg^{-1}). Mean temperature in the laboratory over the study was 19.3 ± 1.6 °C (mean minimum and maximum temperatures were 9.3 ± 1.7 °C and 24.2 ± 2.8 °C). The position of the trays was randomly changed every third day. The trays were watered every four days until leaking through the litter and mineral soil was observed (150 ml each); this amount may seem excessive in comparison to mean annual rainfall in the study region (1200–1300 mm), but it was required to ensure litter saturation at least for a few hours.

Seedling emergence was recorded when the plumule appeared on the forest floor, and was monitored every three days during the first month (June), and at weekly and biweekly intervals afterwards. The experiment was terminated after 145 days, as no further emergence was recorded over a period of two weeks. The seedlings were then removed from the trays and their roots washed. The following growth variables were recorded: total number of leaves ($>$1 cm long), maximum height (root collar up to apical meristem), basal stem diameter at the root collar, length of longest root, and dry weight (root and aerial parts; oven-dried at 75 °C for 72 hr). Germination, early growth of the radicle and plumule before emergence, and seedling emergence through litter were observed in 16 transparent glass boxes (33×20×10 cm; one for each combination of experimental factors); these observations were not replicated.

Analysis

Total emergence, survival (number of surviving seedlings/number of emerged seedlings), establishment (number of surviving seedlings/number of acorns), and root/shoot ratios were transformed to the arcsine of the square root of their proportional values; growth data were log10-transformed (Sokal and Rohlf 1995). Statistical analyses were performed with SPSS 8.0 software. The general factorial procedure (three factors, three replicates) and *a posteriori* comparison tests (Tukey tests) were used on these transformed continuous variables. The shape of the curves built from counts of emerged seedlings through time was compared with a survival function (Fox 1993); the Wilcoxon-Gehan statistic was used for pairwise comparisons (Anonymous

Table 1. Results of ANOVA on the influence of forest floor factors (litter type, T, litter cover, C, litter depth, D, and their interactions) on total seedling emergence (TSE), seedling establishment (SES), length of longest root (LLR), and root/shoot ratio (RSR).

Source of variation	*df*	TSE		SES		LLR		RSR	
		SS	*F*	SS	*F*	SS	*F*	SS	*F*
T	1	0.121		0.016		0.119	2.17 NS	0.219	12.75***
C	1	0.489		0.654		1.042	0.83 NS	0.196	2.86 NS
D	3	0.539		0.222		0.045	6.36**	0.049	3.81*
T × D	3	0.245		0.100		0.156	0.95 NS	0.231	4.49**
T × C	1	0.127		0.108		0.095	0.17 NS	0.012	0.72 NS
D × C	3	0.069		0.045		0.207	1.26 NS	0.006	0.99 NS
T × C × D	3	0.114	3.13*	0.215	4.02*	0.167	1.02 NS	0.071	1.37 NS
Error	32	0.390		0.569		1.748		0.497	

* = ($P \leq 0.05$), ** = ($P < 0.01$), *** = ($P < 0.001$), NS = ($P > 0.05$).

1997). The number of leaves was analyzed with separate Kruskal-Wallis tests for each factor (Sokal and Rohlf 1995).

Results

Total seedling emergence and establishment were significantly affected by the interaction of litter type, litter cover, and litter depth (Table 1, Figure 1); results of *F*-tests on first-order interactions and main effects are not reported (see Underwood 1997). The effect of increasing litter depth on emergence and establishment was more evident in those treatments involving uncovered seeds on pine litter; differences between covered and uncovered samples were larger with a thicker layer of pine litter (Figure 1). The highest emergence and establishment occurred on acorns sowed on mineral soil and covered with a mat of pine litter (Figure 1). The interaction between litter cover and depth did not show any trend in treatments with oak litter.

Seedling survival was not affected by main factors or their interactions ($P > 0.05$). However, a trend towards higher survival was observed when the acorns were covered as compared to uncovered (71.8 ± 3.1% vs. 54.8 ± 5.6%; $0.05 < P < 0.1$). The curves of seedling emergence through time were affected by all three factors, emerging faster when the seeds were placed on mineral soil (Wilcoxon-Gehan $\chi^2 = 56.6$, df = 3, $P < 0.001$), without a cover of litter ($\chi^2 = 11.5$, df = 1, $P < 0.001$), and on pine litter ($\chi^2 = 24.7$, df = 1, $P < 0.001$; Figure 2).

At the end of the experiment (145 days) we found that maximum height and basal diameter of seedlings were not affected by litter cover, litter depth,

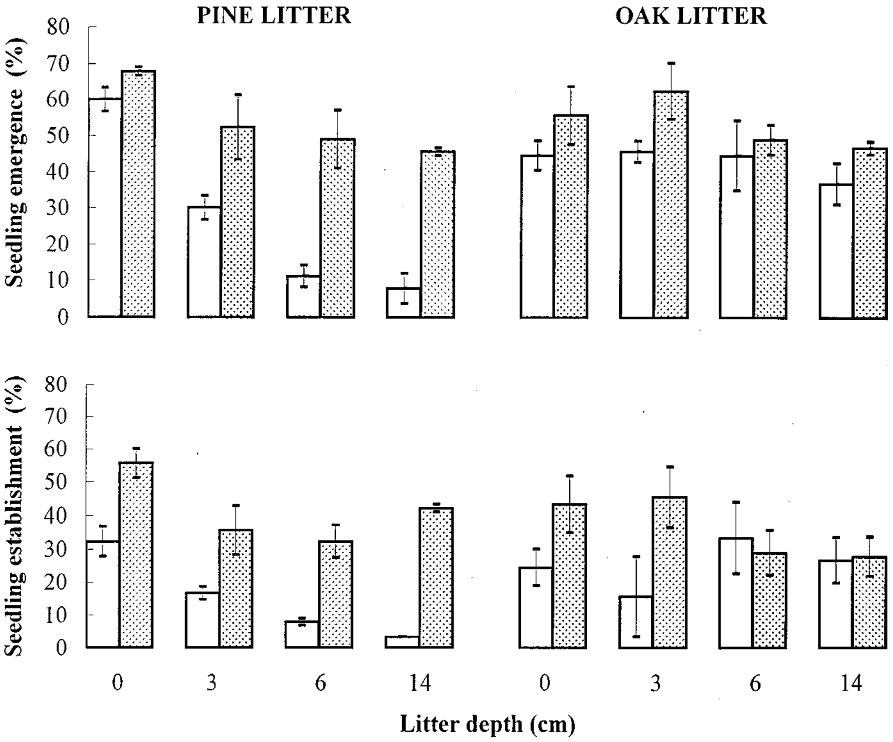

Figure 1. Emergence and establishment of seedlings of *Q. rugosa* (percent average ±1 s.e.) under different litter types (pine needles or oak leaves), litter depth (0, 3, 6, and 14 cm), and litter cover (white bars: uncovered; shaded bars: with a 3 cm cover).

litter type, or their interactions ($P > 0.05$). However, increasing litter depth had a positive effect on the length of the longest root ($P < 0.05$; Tables 1 and 2). The root/shoot ratio was affected by litter type and depth, and their interaction (Table 1). Seedlings growing through oak litter allocated more biomass to roots than to the shoot as litter depth increased; this trend was not found in seedlings growing on pine litter (Table 2). The number of leaves was only affected by litter composition (Kruskal-Wallis test, χ^2 =10.16, df = 1, $P < 0.05$), with higher numbers of leaves in seedlings growing on pine litter (4.17 ± 0.19 vs. 3.24 ± 0.16 leaves).

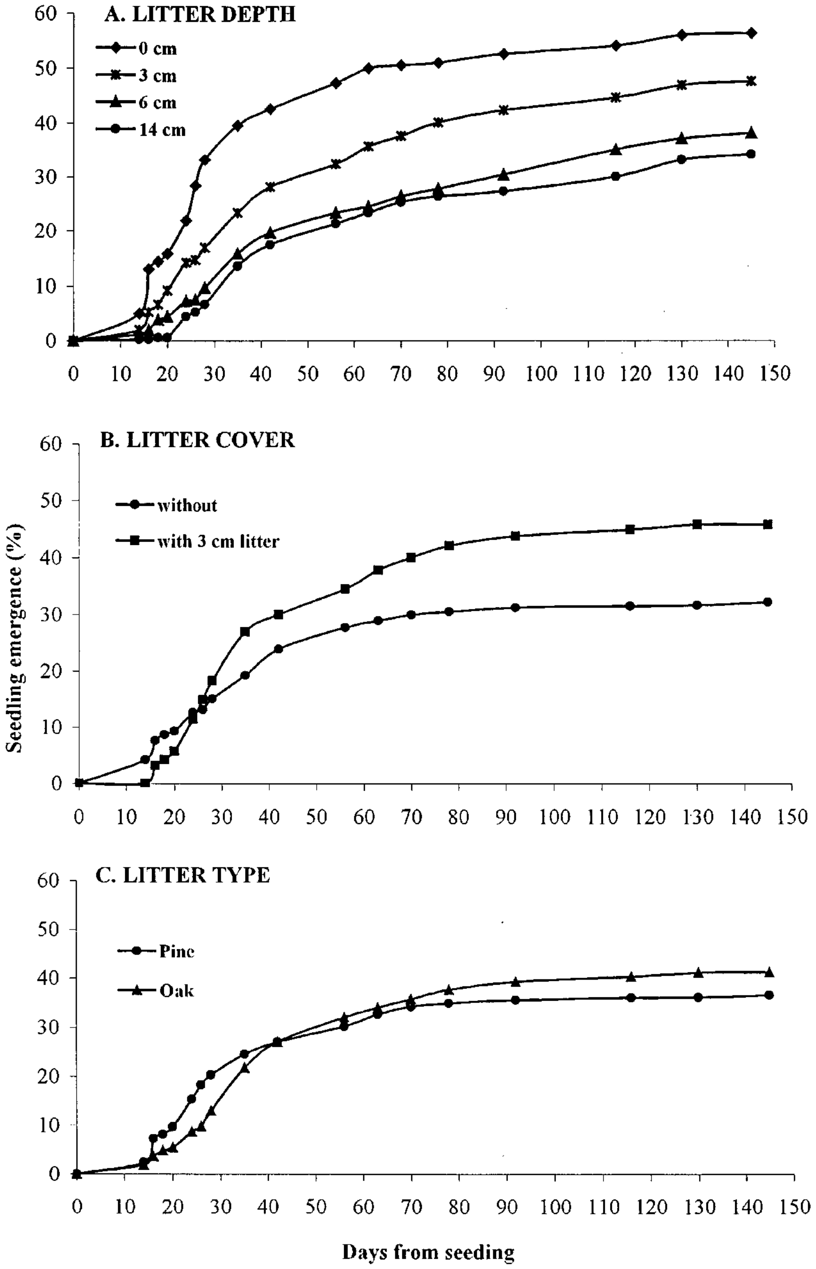

Figure 2. Emergence of seedlings of *Q. rugosa* (percent average) through time as a function of forest floor factors: (a) litter depth, (b) litter cover, and (c) litter type.

Table 2. Mean (±1 s.e.) of seedling survivorship (SSS), maximum height of seedlings (MXH, cm), basal diameter (BDI, cm), length of longest radicle (LLR, cm), and root/shoot ratio (RSR) as a function of litter type (1 = pine, 2 = oak), litter cover (1 = uncovered, 2 = covered), litter depth (1 = 0, 2 = 3, 3 = 6, 4 = 14 cm) and their interactions. Values followed by the same letter are not significantly different ($P > 0.05$).

Factor	Level	n	SSS	MXH	BDI	LLR	RSR
Type	1	202	64.6 ± 4.9 a	16.4 ± 0.6 a	0.093 ± 0.006 a	12.3 ± 0.5 a	0.42 ± 0.03 b
	2	221	62.0 ± 4.7 a	15.3 ± 0.6 a	0.084 ± 0.006 a	13.8 ± 0.4 a	0.61 ± 0.03 a
Cover	1	143	54.8 ± 5.5 a	15.9 ± 0.7 a	0.094 ± 0.009 a	12.6 ± 0.5 a	0.51 ± 0.04 a
	2	280	71.8 ± 3.1 a	15.7 ± 0.5 a	0.085 ± 0.004 a	12.7 ± 0.3 a	0.52 ± 0.02 a
Depth	1	140	68.0 ± 5.6 a	16.8 ± 0.6 a	0.103 ± 0.009 a	9.4 ± 0.4 c	0.43 ± 0.03 b
	2	102	57.3 ± 7.9 a	17.0 ± 0.8 a	0.086 ± 0.005 a	12.8 ± 0.5 b	0.43 ± 0.04 b
	3	92	67.6 ± 4.5 a	13.9 ± 1.0 a	0.076 ± 0.009 a	13.7 ± 0.6 b	0.52 ± 0.05 b
	4	89	60.4 ± 9.0 a	14.8 ± 1.0 a	0.079 ± 0.006 a	16.4 ± 0.6 a	0.68 ± 0.06 a
Type × Cover	1 × 1	53	52.1 ± 7.5 a	17.6 ± 0.9 a	0.105 ± 0.018 a	12.1 ± 0.9 a	0.37 ± 0.07 a
	1 × 2	149	77.1 ± 3.7 a	15.9 ± 0.6 a	0.087 ± 0.004 a	12.3 ± 0.4 a	0.47 ± 0.03 a
	2 × 1	90	57.5 ± 8.4 a	14.8 ± 0.9 a	0.085 ± 0.009 a	13.4 ± 0.6 a	0.66 ± 0.05 a
	2 × 2	131	66.4 ± 4.4 a	15.5 ± 0.8 a	0.082 ± 0.007 a	13.1 ± 0.5 a	0.57 ± 0.03 a
Type × Depth	1 × 1	79	69.2 ± 7.5 a	17.5 ± 1.0 a	0.110 ± 0.009 a	9.3 ± 0.6 a	0.42 ± 0.04 a
	1 × 2	47	62.1 ± 4.9 a	16.8 ± 1.3 a	0.095 ± 0.013 a	13.4 ± 0.7 a	0.44 ± 0.06 a
	1 × 3	36	71.0 ± 6.0 a	15.1 ± 1.8 a	0.068 ± 0.017 a	11.9 ± 1.0 a	0.35 ± 0.08 a
	1 × 4	40	72.8 ± 14.0 a	15.6 ± 2.5 a	0.082 ± 0.024 a	14.5 ± 1.5 a	0.46 ± 0.10 a
	2 × 1	61	67.2 ± 8.9 a	15.8 ± 1.1 a	0.102 ± 0.011 a	9.5 ± 0.6 a	0.43 ± 0.05 b
	2 × 2	55	51.9 ± 14.2 a	17.4 ± 1.3 a	0.082 ± 0.012 a	12.7 ± 0.7 a	0.42 ± 0.06 b
	2 × 3	56	64.2 ± 7.3 a	13.5 ± 1.1 a	0.085 ± 0.011 a	14.6 ± 0.7 a	0.70 ± 0.05 b
	2 × 4	49	64.6 ± 7.0 a	13.9 ± 2.0 a	0.070 ± 0.012 a	16.7 ± 0.7 a	0.90 ± 0.05 a
Depth × Cover	1 × 1	50	57.0 ± 8.4 a	16.7 ± 1.2 a	0.118 ± 0.011 a	9.5 ± 0.7 a	0.40 ± 0.05 a
	1 × 2	90	79.4 ± 4.1 a	16.6 ± 0.9 a	0.094 ± 0.009 a	9.4 ± 0.5 a	0.45 ± 0.04 a
	2 × 1	29	44.3 ± 12.8 a	17.5 ± 1.6 a	0.091 ± 0.015 a	13.7 ± 0.9 a	0.44 ± 0.07 a
	2 × 2	73	69.7 ± 2.9 a	16.7 ± 1.0 a	0.085 ± 0.009 a	12.4 ± 0.6 a	0.42 ± 0.04 a
	3 × 1	37	73.1 ± 7.3 a	14.7 ± 1.8 a	0.076 ± 0.017 a	12.4 ± 1.1 a	0.49 ± 0.08 a
	3 × 2	55	62.1 ± 4.9 a	13.7 ± 1.3 a	0.075 ± 0.011 a	14.1 ± 0.7 a	0.56 ± 0.05 a
	4 × 1	27	61.4 ± 12.2 a	14.8 ± 2.6 a	0.073 ± 0.025 a	14.8 ± 1.5 a	0.72 ± 0.07 a
	4 × 2	62	75.9 ± 9.3 a	14.7 ± 1.1 a	0.080 ± 0.010 a	16.5 ± 0.6 a	0.65 ± 0.05 a

Discussion

Effects of litter on seedling establishment

The emergence and early growth of *Q. rugosa* were influenced by litter cover, litter depth, and litter type under laboratory conditons. A deep and dense mat of litter may: (1) interfere with downward movements of seeds through the litter layers before germinating (Facelli and Pickett 1991a), (2) impose a mechanical barrier against radicle penetration (Ahlgren and Ahlgren 1981; Facelli and Pickett 1991a; Peterson and Facelli 1992), (3) modify the soil moisture content through reducing water infiltration and evaporation (Facelli and Pickett 1991a), (4) alter the decomposition of organic matter and the cycling of soil nutrients (McClaugherty et al. 1985), (5) intercept light that could otherwise reach the cotyledons and the plumule (Facelli and Pickett 1991b), and (6) increase the chances of seed exposure to pathogens and insect predators (Itoh 1995). In this study, emergence on pine litter was markedly affected by litter depth and cover (Figure 1), suggesting that a mat of pine needles may have a lower water retention capacity in comparison to oak leaves.

Our results indicate that a litter cover on the acorns may favor their germination and early establishment, especially if they are sowed on a pine seedbed. Barrett (1931) found that recently fallen oak leaves that formed a layer of 2.5–5.0 cm on the acorns of *Q. montana* (*Q. prinus* in southern Appalachian forests) favored establishment. We observed that acorns sowed on a seedbed of oak leaves usually moved downwards and remained covered by one or several layers of leaves. On the other hand, acorns sowed on pine needles remained on the surface and, consequently, were more exposed to desiccation.

The composition and structure of litter may affect the time elapsed between seed germination and emergence of seedlings. The forest floor in pinelands includes a relatively homogenous and finely interwoven layer of pine needles. In contrast, seedbeds in oak forests are composed by a thick, loose, and heterogeneous layer of relatively large oak leaves (in our study area the foliage includes *Q. candicans*, *Q. crassifolia*, *Q. crispipilis*, *Q. laurina*, *Q. rugosa*, and *Q. skutchii*, in addition to leaves of 20–30 broadleaved species; González-Espinosa et al. 1995). Differences in the structure of the litter layers affected the rate of seedling emergence: the plumules of seedlings growing through pine litter emerged earlier (18 days after sowing) than those sowed on oak litter (25 days). Observations of acorns through transparent glass boxes indicated that after 18 days they attained similar germination if sowed on pine (12%) or oak litter (15%). The delay in emergence can be accounted for by the etiolation and horizontal growth of plumules and radicles through several layers of oak litter; the etiolated seedlings were 4–5 times longer (12–15 cm long) than seedlings germinating closer to the surface of the forest floor after 25 days (2–3 cm). Similar responses with broadleaved litter have been reported from eastern North America on *Q. montana* (Barrett 1931), *Betula alleghaniensis* (Peterson and Facelli 1992), and *Pinus taeda* (Shelton 1995).

Seeds sowed on exposed mineral soil showed abundant and fast emergence, as found in other oaks (Carvell and Tryon 1961). However, bare soil may become unfavorable for germinating acorns because of high temperatures (Borchert et al. 1989), freezing (Facelli and Pickett 1991a), and removal by predators (Shaw 1968; Bonfil and Soberón 1999). In this study, the most abundant emergence was recorded when acorns were sowed on mineral soil covered with 3 cm of pine litter (Figure 1), confirming the beneficial joint effect of these two factors (Ahlgren and Ahlgren 1981).

Litter type affected the allocation of biomass to shoots and roots; however, this did not reflect on seedling survival of *Q. rugosa* seedlings within the period of the study. The larger root/shoot ratio of seedlings growing on oak litter may allow them in the future to tolerate soil drought, nutrient deficiency, and damage by browsers (Larsen and Johnson 1998).

Management implications

Pinelands offer favorable microsites for the natural establishment of oaks (Mosandl and Kleinert 1998). Seedlings growing in the relatively open pinelands may be exposed to a well lighted (Crow 1988) and low-competitive environment (Tripathi and Khan 1990). Oak seedlings and saplings may occasionally abound in pinelands within the study region, provided that acorns are available from nearby oak-dominated forests (Galindo-Jaimes 1999). Survival of seedlings of *Q. laurina* after 18 months from direct seeding was highest ($>$50%) in pinelands as compared to pine-oak and old-growth forests (Camacho-Cruz et al. 2000). Results of this study and previous reports lead us to consider as feasible the establishment of oak seedlings in pinelands having a shallow or moderately deep litter layer (3–6 cm), where also seed-eating rodents and birds may be scarce (Schupp 1988; Quintana-Ascencio et al. 1992).

Planting oak seedlings (at least one-year old) may be a reliable but expensive practice. A low-cost alternative may use direct seeding of scarified acorns under a cleared understory. However, more field research is needed to define a restoration practice following from this study. Suggested treatments may include: (1) removing the litter to sow the acorns on a seedbed of mineral soil, and (2) covering the acorns with a 3 cm layer of litter.

Acknowledgements

We thank N. Ramírez-Marcial, P.F. Quintana-Ascencio, Z. Cano-Santana, T. Valverde-Valdés, C. Bonfil-Sanders, B.L. Haines, J. Zasada, and three anonymous reviewers for valuable comments. M. Martínez-Icó, A. Luna-Gómez, and E. Fuentes (fellowship from the Academia Mexicana de Ciencias) helped with locating sites and labor. We also thank M. Jiménez-Heredia (Mitzitón), M. Martínez-Alvarez (Rancho Merced-Bazom), and R. Domínguez and J. Rabasa (PRONATURA-Chiapas) for access to sites.

Research supported by ECOSUR and the University of Georgia/ECOSUR exchange program (to B. Berlin).

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