



Synergistic responses of oak, pine and shrub seedlings to edge environments and drought in a fragmented tropical highland oak forest, Oaxaca, Mexico

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Abstract

Processes of natural regeneration in highly fragmented landscapes are strongly influenced by edge environments due to the effects of vegetation cover on microclimate conditions. These effects may be diminished or exacerbated through synergistic interactions with extreme climatic events such as drought. This study assessed the growth and physiological responses of five native tree and shrub species (*Quercus acutifolia* Neé, *Q. castanea* Neé, *Pinus oaxacana* (Mart.) Mirov, *Dodonea viscosa* (L.) Jacq., *Rhus virens* Adams) to microsites along edge gradients occurring between forest remnants and openings of different sizes (<0.1 and >1 ha) in both a highly fragmented and a relatively undisturbed adjacent landscape over a 2-year period (1 year with normal rainfall and one with extreme drought). Of the species studied, the shrub seedlings had significantly lower mortality (3–13%) than the oak (37–53%) and pine (35%). Seedling survival for all species was greatest in the edge and forest understory environments, suggesting that vegetation cover may have a facilitative effect on seedling regeneration. Greater survivorship and biomass of the shrub seedlings, especially in the open microsites, was attributed to their root system having a sufficient biomass and depth to more effectively access deeper water supplies. Interactions between edge effects and an extreme drought event were found to have a more pronounced impact on the performance of oak and pine seedlings compared to shrub seedlings. Patterns of pre-dawn water potential ($\psi_{pd} < -3.8$) and leaf phenology (slow turnover) indicated that oak species experienced high water stress that prevented their successful establishment in open environments, especially during drought years. In contrast, shrub seedlings, and to a lesser extent pine seedlings, maintained higher pre-dawn moisture potentials ($\psi_{pd} > -2.9$) and greater phenological plasticity (fast turnover) in response to drought, contributing to greater growth and survival success. To effectively manage fragmented tropical highland oak forest landscapes for reestablishment of the native oak ecosystem, there is a need to understand the complex and often synergistic interactions between different plant species, the edge environment, and climatic variability that strongly influence regeneration processes.

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Keywords: *Dodonea viscosa*; Dry tropical highlands; Drought; Habitat fragmentation; Mexico; Oak forests; *Pinus oaxacana*; *Quercus acutifolia*; *Q. castanea*; Regeneration; *Rhus virens*

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1. Introduction

Studies in both temperate and tropical regions have documented how habitat fragmentation modifies regeneration dynamics and species composition of vegetative communities, and subsequently how existing species respond to new disturbances occurring at decadal time scales (Wilcox and Murphy, 1985; Saunders et al., 1991; Sarmiento, 1997; Ferreira and Laurance, 1997; Laurance, 2000; Doak et al., 1992; Turner et al., 1998; Bunnell and Huggard, 1999; Martinez-Garza and González-Montagut, 1999). Expression of ecological processes in fragmented landscapes is strongly determined by the predominance of edge environments between adjacent vegetation communities that formed following disturbance events. These edges can control changes in microclimatic conditions as well as the distribution and availability of resources required by plants to establish and grow (e.g., Forman and Godron, 1986). Edges represent the boundary across which regeneration of plant species typical of a mature forest must eventually reestablish if habitat recovery is to occur (Chen et al., 1992; Matlack, 1994; Benitez-Malvido, 1998; Burke and Nol, 1998; Euskirchen et al., 2001; Gelhausen et al., 2000; Laurance, 2000).

Regeneration in fragmented landscapes may also be strongly influenced by existing vegetation cover. Seedling growth may be enhanced when growing at forest edges or in the understory due to the ameliorating effects of mature trees and shrubs on abiotic microsite conditions (Castro et al., 2002). The main facilitative effect may result from shading, which protects seedlings against high irradiance and temperatures but also results in higher soil moisture levels due to lower evapotranspiration rates under shade (Joffre and Rambal, 1988; Belsky et al., 1989; Breashears et al., 1997). Deeply rooted trees and shrubs may also enhance water availability through hydraulic lifting processes (Richards and Caldwell, 1987; Caldwell and Richards, 1989; Dawson, 1993). Since moisture availability is often the most important determining factor affecting plant establishment and growth following disturbance in dry climatic regions (Gordon et al., 1989; Barton, 1993; Pugnaire and Haase, 1996; Páez and Marco, 2000; Zavala et al., 2000; Meentemeyer et al., 2001), edge environments may provide critical regeneration sites in fragmented

landscapes. However, tree cover may also *decrease* soil moisture availability due to higher levels of transpiration and water uptake by mature trees in more dry climates (Joffre and Rambal, 1993; Belsky et al., 1993; Breashears et al., 1997). Thus, site-specific interactions between climate, vegetation, and disturbance may lead to differential effects on seedling regeneration processes; however, these effects have not been adequately examined (Asbjornsen et al., in press).

Oak forests historically dominated a large portion of the tropical and subtropical highlands of Mexico, Central America, and South America and have been areas of human settlement for centuries. Today these forests are severely fragmented due to land conversion to agricultural and grazing, combined with harvesting of trees for a variety of purposes (Rzedowski, 1978; Gonzalez-Espinosa et al., 1991; Quintana-Ascencio et al., 1992; Nixon, 1993). However, in recent decades some tropical highland regions, such as in southeastern Mexico, have experienced reductions in human population pressures due to increased out-migration and shifts in local livelihood strategies towards external employment and market opportunities. These changes in land use patterns and population dynamics may be creating new opportunities for the regeneration and restoration of the native highland oak forests. However, a major unknown is whether tropical highland oak forests are sufficiently resilient to successfully reestablish on areas where the original forest cover has been removed due to previous land use activities and where abiotic and biotic conditions have been drastically altered (Gonzalez-Espinosa et al., 1991).

While oak species native to temperate moist climates have been widely studied, and a large knowledge base exists on their shade tolerances, drought adaptations, and regeneration characteristics (e.g., Johnson et al., 2002, and references therein), a paucity of research has been conducted on oak forests common to tropical highland regions. The unique environmental conditions of these high-elevation tropical mountains (e.g., highly seasonal rainfall, long growing season, high irradiance) preclude transferring much of the research already conducted in other mountainous regions located at middle-latitudes (Leuschner, 2000). In particular, our understanding is limited of how edges affect microclimate and regeneration processes in fragmented landscapes, and the implications of these interactions for management practices aimed

at achieving long-term resilience and sustainability of high-elevation tropical forests.

Our study was conducted in fragmented landscapes supporting seasonally dry tropical oak forests in south-eastern Mexico. We hypothesized that the capacity and rate at which oak seedlings and other native plant species successfully reestablish the successional pathways to form native oak forests in highly fragmented landscapes (i.e. pre-dating the period of the intensive land use) will be strongly determined by their ability to adapt to the range of microclimatic conditions existing across edge environments. To understand the underlying mechanisms affecting successional processes, we designed our study to answer the following questions: (1) Do plant species from different successional seres vary in their establishment success and growth response to different microclimate conditions occurring across edge environments? (2) Does the degree of habitat fragmentation (i.e., forest cover loss) influence species' response to edge microsites? (3) Can differences in species' physiological adaptations to moisture stress explain differences observed in their growth performances? When a severe drought occurred in 1997–1998, the following question was added: (4) Do severe drought events create synergistic interactions with existing landscape patterns that can lead to shifts in individual plant species' responses and long-term successional trajectories?

2. Site description

This research was conducted in the Mixteca Alta region of Mexico, located in the Nochixtlán District in the southeastern State of Oaxaca in southeastern Mexico, at approximately 17°N latitude. The study area is characterized by mountainous topography, comprised primarily of sedimentary, igneous and metamorphic geological formations (Ferrusquia-Villafraña, 1976), while the primary soil types include lithosols, regosols, cambisols, and small areas with andisols (García-Mendoza and Cruz, 1993). Climate is seasonal with a 6–8-month dry season (November–April), with mean annual precipitation ranging between 450 and 800 mm (for a more detailed description, see Asbjornsen et al., in press).

The study plots were located in the communal forests belonging to two adjacent villages (San Pedro

Cántaros Coxcaltepec and Santiago Huaucuililla), characterized by different land use histories and, subsequently, degrees of forest removal and fragmentation: in San Pedro Cántaros, the high fragmentation site, a long history of forest clearing for agriculture and grazing has created a landscape matrix dominated by open clearings, interspersed with small forest remnants that often have a high degree of patchiness due to small openings resulting from harvesting of trees for fuelwood and charcoal production. Most of the large clearings had been abandoned during the past 8–10 years; however, charcoal production continues today within many of the forest remnants.

The dominant vegetation type at the two study sites was drought deciduous oak forest typically occurring between 1500 and 2500 m elevation with an average canopy tree height of 10–15 m (Salas et al., 1994). Dominant mature forest species included: *Quercus acutifolia* Neé, *Q. segouiensis* Liebm., *Quercus castanea* Neé, *Juniperus deppeana* Adams, and *Arbutus glandulosa* DC. Vegetative cover in the clearings was predominantly grasses and forbs, although the following successional woody species often occurred, especially along the edges: *Pinus oaxacana* (Mart.) Mirov, *P. lawsonii* Roehl ex Gord., *Rhus virens* Gray, *Baccharis conferta* H.B.K., *Arctostaphylos pungens* Kunth., *Dodonaea viscosa* (L.) Jacq., and *J. deppeana* Adams. Although plant species composition was similar at the two sites, forest structure varied due to their different land use histories: Huaucuililla supported predominantly mature old growth forest, while Cántaros had young successional forest with the majority of the trees regenerating from stump sprouts. Based on the similar biophysical and climatic conditions existing at the two sites, we assumed that the original vegetation cover prior to land use activities had also been similar. In the absence of extant interior forest habitat, the relatively less disturbed mature forests in the low fragmentation site served as 'reference' conditions to which the high fragmentation site was compared.

3. Materials and methods

3.1. Experimental design

The study design consisted of three replicate plots established for each of the following types of forest

openings in the summer of 1994: (1) ‘small’ openings (<0.1 ha), (2) ‘large’ openings (>1.0 ha) in the highly fragmented landscape of Cántaros, and (3) ‘reference’ openings within the less fragmented landscape of Huaucilla (<0.1 ha). Each plot was stratified by the following four microsities (subplots) located along a transect from the center of the forest opening into the forest interior perpendicular to the south facing edge: (1) ‘open’ (approximate center of the clearing), (2) ‘outer-edge’ (5 m into the shrub vegetation from the forest edge), (3) ‘inner-edge’ (5 m into the forest vegetation from the forest edge), and (4) ‘forest’ (30 m into the forest vegetation from the forest edge). At each microsite within each of the nine patches, a 4 m × 1 m fenced enclosure was constructed of chicken wire (mesh size = 2.5 cm) in February 1996; the long side of each enclosure was positioned parallel to the forest edge in order to minimize environmental variability within each enclosure due to edge effects. Fenced enclosures were needed to protect transplanted seedlings from trampling and grazing damage by animals, as well as from disturbance by humans.

Seedlings of five native plant species belonging to three different successional seres were grown from seed in a tree nursery located in the community of San Pedro Cántaros: *Dodonea viscosa* (L.) Jacq. and *R. virens* Gray (early successional shrub species), *P. oaxaca* (Mart.) Mirov (mid-successional tree species), *Q. acutifolia* Neé and *Q. castanea* Neé (mature canopy late-successional tree species). Seeds were collected from trees growing at the study site, either directly from the plants (*D. viscosa*, *R. virens*, and *P. oaxacana*) or as freshly fallen acorns (*Quercus* spp.). Seeds were sown in seedbeds containing a 1:2:1 mixture of sand, soil and forest humus. The forest humus was collected from sites dominated by the corresponding plant species for which it was being used, to ensure that the appropriate mycorrhizal fungal inoculum was present. Once germinated, seedlings were transplanted to polyethylene bags containing the same soil mixture. In June 1996, seedlings (with the soil growth medium intact) were transplanted from the polyethylene bags into the fenced enclosures; this minimized disturbance to the roots and reduced transplant shock. Seedlings were planted within the enclosures according to a random systematic design with a minimum of 20 cm spacing between seedlings. The

number of seedlings planted per enclosure varied according to availability of plants: 8–10 *Quercus* spp. and *P. oaxacana*, nine *D. viscosa*, and four *R. virens*. A buffer zone of 20 cm was maintained between the seedlings and the fence.

Seedling growth was monitored every 6 months (during both wet and dry seasons) by measuring seedling height and counting the number of leaves (for pine seedlings, average leaf length was measured rather than number of leaves). Leaf bud production, leaf expansion, and leaf senescence and abscission were recorded every 2 weeks during the dry season (November–May) and monthly during the wet season (June–October). Seedling mortality was recorded at each of the collection times.

Seedlings were harvested in February of 1998, 2 years after out-planting. At the time of harvesting, pre-dawn leaf water potential (ψ_{pd}) was determined for 3–5 seedlings of each species growing in the open and forest microsities for each plot. In cases where there were not enough seedlings of a particular species in a microsite, seedlings were selected from the shrub and edge microsities as representative of the open and forest microsities, respectively. Measurements of ψ_{pd} were taken between 4:30 and 6:30 a.m. using a portable pressure chamber (Plant Moisture Stress Instrument Company, Corvallis, OR, USA). For small seedlings (i.e., oaks and pines) the entire stem was cut and used to determine ψ_{pd} . For large seedlings (i.e., most *D. viscosa* and *R. virens* seedlings) the upper portion of the central stem or a branch was cut and used for the ψ_{pd} measurement. Each seedling was measured immediately after cutting the stem. For statistical analysis, the data were pooled by species and microsite.

After harvesting the seedlings, stem length, total number of leaves, maximum root length, and number of lateral roots were recorded for each seedling. Leaves were cut from the stem at the petiole and leaf area determined for all green leaves using a CI-202 portable leaf area meter (CID Inc., Vancouver, WA). Three repeated measurements were taken for the leaves of each plant and an average used for the final value. For the belowground portion of each seedling, total root length and number of lateral root branches were determined. All plant components were dried to a constant weight at 70 °C and dry weight biomass determined.

Table 1

The statistical model used in the analysis of variance for all response variables

Source	d.f.	Error term used in test
Size	2	Plot(size)
Plot(size)	6	
Microsite	3	Microsite(plot,size)
Microsite × size	6	
Microsite(plot,size)	18	
Species	4	Error
Size × species	8	Error
Micro × species	12	Error
Size × micro × species	24	Error
Error	68	

3.2. Statistical analysis

Analysis of variance for a split plot design (whole-plot = size; subplot = micro; subsubplot = season) was used to test for significant main effects and interactions among treatments on seedling growth, phenology, mortality, and pre-dawn soil moisture (SAS Institute, 1995). For seedling height, relative height increments (calculated as the increase in height between two consecutive recording times) were used in order to account for differences in the initial heights among seedlings at the time of planting (determination of relative values for biomass was not possible due to lack of seedling biomass data at the time of planting). Contrasts were performed within analysis of variance to assess interaction terms and differences between individual treatment effects (see Table 1 for statistical model). When necessary, log-transformations were performed in order to normalize the data or account for the use of percentage data.

4. Results

4.1. Seedling height growth, root length, and biomass accumulation

During the 2-year study period, relative height growth was generally greatest for the two early successional species (*D. viscosa* and *R. virens*), intermediate for *P. oaxacana*, and least for the two mature forest oak species (*Q. acutifolia* and *Q. castanea*), although only differences between the oaks compared to all other species were significant (Fig. 1). All species experienced some die-back, although die-back was especially pronounced for the oak seedlings (data not shown). Comparing across microsites, no strong patterns in height growth were apparent. In contrast, when comparing across opening types, there was a strong trend suggesting greatest height growth in the reference openings, intermediate in the small openings, and least in the large openings (Fig. 1). Maximum root length and number of lateral root branches were greatest for the shrub seedlings, intermediate for the pine seedlings, and least for the oak seedlings (Table 2). Although differences between open and forest microsites were not significant, *D. viscosa* appeared to exhibit some degree of plasticity across the microsites, with greater root length and number of lateral roots produced in the open microsites.

For all species, total seedling biomass was significantly greater for seedlings growing in the open microsites compared to the other three microsites, while biomass for seedlings growing in the forest microsites was generally lowest (Fig. 2). However,

Table 2

Mean (±S.E.) maximum root length and number of lateral branches for seedlings growing in different microsites (open, outer-edge, inner-edge, forest) located along the edge gradient

Species	Root length (cm)		Number of lateral branches	
	Open	Forest	Open	Forest
<i>Q. acutifolia</i>	9.4 (0.9) c	10.3 (0.6) c	1.0 (0.2) b	1.1 (0.1) b
<i>Q. castanea</i>	8.3 (2.0) c	7.9 (0.3) c	0.3 (0.2) b	0.4 (0.1) b
<i>P. oaxacana</i>	11.5 (1.4) ab	10.1 (0.3) c	1.6 (0.5) b	0.9 (0.1) b
<i>D. viscosa</i>	14.6 (0.4) a	13.6 (1.1) a	3.9 (0.3) a	3.5 (0.4) a
<i>R. virens</i>	12.4 (0.7) ab	12.3 (0.9) ab	3.3 (0.2) a	4.2 (0.3) a

Lower case letters indicate significant differences across both rows and columns by plant component, using Tukey–Kramer adjustment for pair-wise comparisons.

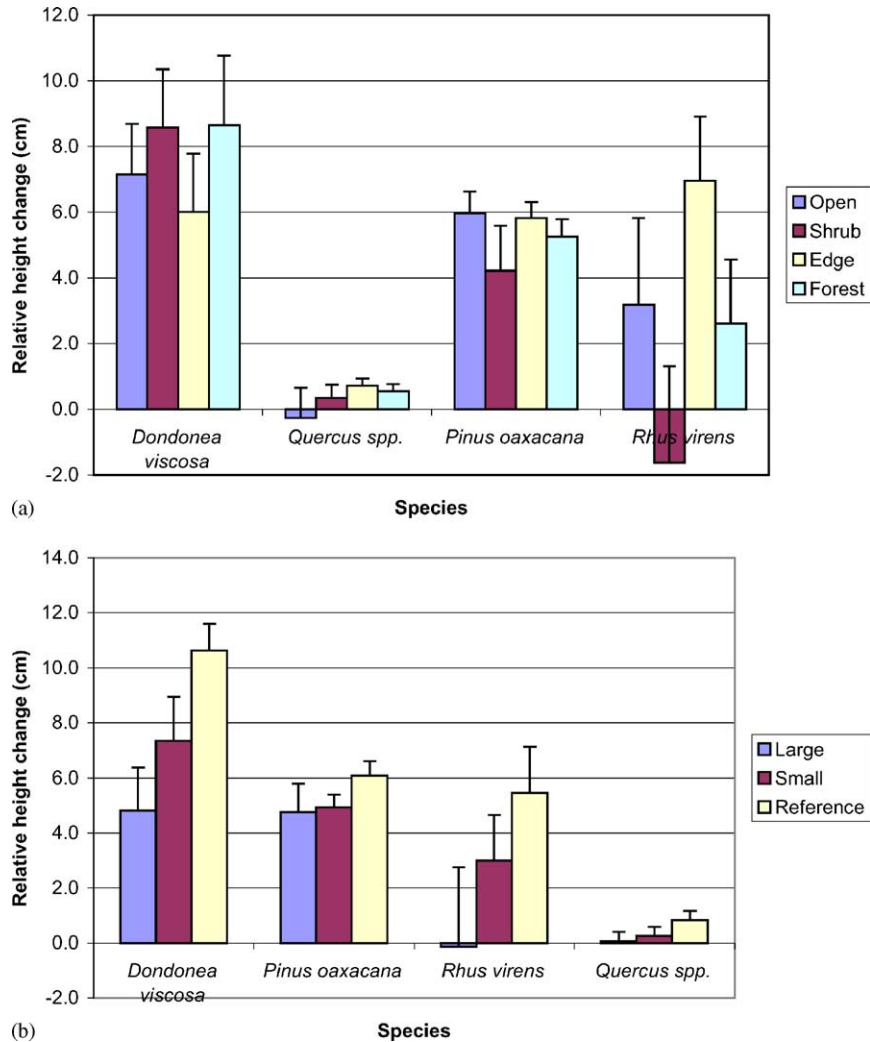


Fig. 1. Mean (\pm S.E.) total relative height increment (final height – initial height) for seedlings of four species (data for *Q. acutifolia* and *Q. castanea* combined), comparing across different: (a) microsites (open, shrub, edge, forest) and (b) opening size (large, small, and reference).

there were no consistent patterns in biomass across different opening sizes, although the exceptionally high biomass of pine seedlings growing in the large openings was notable. As expected, there were big differences in biomass among species, with the oaks having the lowest biomass and the shrubs having the highest biomass across microsites (Table 3). For the oak species, differences in total seedling biomass were primarily explained by differences in root biomass, since biomass of leaves and stems did not vary greatly among microsites (Table 3). For the pine and *R. virens*

seedlings, biomass of all plant components (stem, leaves, and roots) was greater for seedlings growing in the open and shrub microsites, compared to edge and forest microsites. Similar trends were observed for *D. viscosa*, except that stem biomass did not vary among microsites.

Biomass allocation patterns varied among species and microsite location (Table 3). Oak seedlings allocated greater biomass to roots (58–77%) and least to leaf biomass (4.9–18%) compared to all other species. Greatest allocation to roots occurred in oak seedlings

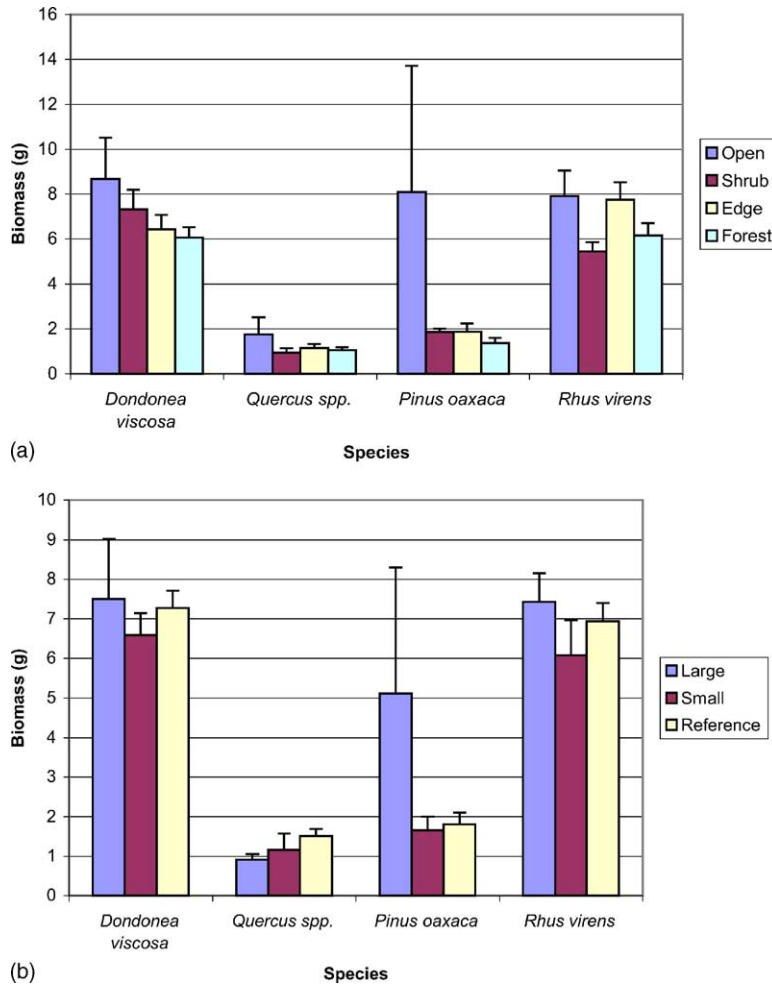


Fig. 2. Means (\pm S.E.) total seedling biomass for seedlings of four species (data for *Q. acutifolia* and *Q. castanea* combined), comparing across different: (a) microsites (open, shrub, edge, forest) and (b) opening size (large, small, and reference).

growing in the shrub microsites. For pine seedlings, only 24–34% of total biomass was allocated to the roots, with highest values occurring in the forest microsites. Pine seedlings allocated between 40 and 50% of total plant biomass to leaf tissue, representing at least 20% greater allocation to leaf tissue compared to the other species. *D. viscosa* allocated between 35 and 39% of total plant biomass to roots, 45 and 50% to stem tissue, and 12 and 16% to leaf tissue, with seedlings in the open microsites having greatest allocation to both roots and leaves compared to the other microsites, although differences between microsites were not great. Compared to other species, *D. viscosa*

seedlings allocated at least 50% more biomass to stem tissue. *R. virens* allocated a relatively large proportion of total plant biomass to roots (47–60%), while only 16–27% was allocated to leaves, and 23–31% to stems.

Total seedling leaf area was greatest for the two shrub species (43.4–109.5 cm²) and least for the oaks (4.4–15.1 cm²), however differences among species were only significant for oak seedlings growing in the edge and forest microsites (Table 4). Individual leaf area was smallest for the oak species (1.6–2.9 cm²), intermediate for *D. viscosa* (3.6–5.1 cm²), and greatest for *R. virens* (5.7–13.5 cm²) (only values for *R. virens*

Table 3

Means (\pm S.E.) seedling biomass and % allocation after two growing seasons by plant component and for total above ground and plant biomass, for seedlings growing in different microsites (open, outer-edge, inner-edge, forest) located along the edge gradient

Species and material	Open		Shrub		Edge		Forest	
	x (g)	%	x (g)	%	x (g)	%	x (g)	%
<i>Q. acutifolia</i>								
Leaves	0.2 f (0.1)	11.8	0.1 f (0)	10.0	0.2 f (0.1)	15.4	0.1 f (0)	9.1
Roots	1.1 c (0.5)	58.8	0.7 cd (0.2)	70.0	0.8 c (0.1)	61.5	0.8 c (0.1)	72.7
Stem	0.3 de (0.1)	17.6	0.2 e (0)	20.0	0.3 de (0.1)	23.1	0.2 d (0)	18.2
Total	1.7 b (1.0)		1.0 bc (0.2)		1.3 b (0.2)		1.1 b (0.1)	
<i>Q. castanea</i>								
Leaves	0.2 ef (0.1)	15.4	0 ne (0)	0	1.0 f (0.2)	15.6	0.1 f (0)	16.7
Roots	0.8 c (0.2)	61.5	0.6 d (0)	85.7	2.2 d (0.2)	34.4	0.5 d (0.1)	83.3
Stem	0.4 de (0.3)	30.8	0.1 ne (0)	14.3	3.2 f (0.3)	50.0	0.1 f (0)	16.7
Total	1.3 b (0.2)		0.7 ne (0)		6.4 c (0.7)		0.6 c (0.1)	
<i>P. oaxacana</i>								
Leaves	3.6 a (2.4)	45.2	0.9 abcd (0.1)	50.5	1.0 cd (0.3)	52.7	0.6 de (0.1)	47.0
Roots	2.3 c (1.8)	28.6	0.5 cd (0)	25.0	0.4 d (0.1)	20.24	0.4 d (0.1)	30.1
Stem	2.1 bc (1.5)	26.2	0.5 d (0.1)	24.5	0.5 d (0.1)	27.02	0.3 de (0.1)	22.9
Total	8.1 a (5.6)		1.9 b (0.2)		1.9 b (0.4)		1.4 b (0.2)	
<i>Dodonea viscosa</i>								
Leaves	1.5 abcd (0.4)	17.5	1.1 abcd (0.2)	15.0	1.0 abcd (0.2)	25.5	0.8 bcd (0.1)	19.1
Roots	3.3 ab (0.6)	37.4	2.7 abc (0.3)	36.4	2.2 bc (0.3)	46.1	2.3 bc (0.2)	57.5
Stem	3.9 a (0.8)	45.1	3.6 a (0.5)	48.6	3.2 a (0.3)	28.3	3.1 ab (0.3)	23.4
Total	8.6 a (1.8)		7.3 a (0.9)		6.4 a (0.7)		6.1 a (0.5)	
<i>R. virens</i>								
Leaves	1.9 abc (0.5)	19.3	0.9 abcd (0.1)	16.1	2.0 ab (0.3)	25.6	1.2 abcd (0.2)	17.4
Roots	4.4 a (0.5)	55.4	2.8 abc (0.3)	52.9	3.6 ab (0.6)	47.0	3.5 ab (0.1)	59.5
Stem	1.8 abc (0.3)	25.3	1.5 bc (0.2)	31.0	2.2 abc (0.2)	27.4	1.4 bc (0.2)	25.3
Total	8.1 a (1.1)		5.2 a (0.4)		7.7 a (0.8)		6.1 a (0.4)	

Lower case letters indicate significant differences across both rows and columns by plant component, using Tukey–Kramer adjustment for pair-wise comparisons.

in the forest and edge microsites were significantly different). For all species, leaf area was greater when plants were growing in the forest understory compared to the open microsites. In contrast, leaf mass was greatest for seedlings growing in open microsites, with highest mass recorded for *Q. acutifolia* (35.3 mg/cm²), followed by *R. virens* (24.9 mg/cm²) and *Q. castanea* (20.8 mg/cm²), and *D. viscosa* having the lowest leaf mass (15.3 mg/cm²). Due to the low sample size for the oak seedlings caused by high mortality rates, differences could not be detected statistically. Leaf mass for the oak seedlings declined

sharply for the other three microsites (7.4–12.9 mg/cm²), while leaf mass in the shrub species did not differ greatly among microsites.

4.2. Phenology

Seedling phenology showed strong patterns associated with both microsite location and season, and varied by species. Data on the relative change in the number of leaves indicates that leaf turnover was greatest for the two shrub species, although the temporal dynamics of leaf change varied: *D. viscosa* had a

Table 4
Mean (\pm S.E.) individual leaf area, leaf mass, and total plant leaf area comparing between four plant species growing in two different microsites (open, forest) along the edge gradient

	Individual leaf area (cm ²)				Leaf mass (mg/cm ²)				Total plant leaf area (cm ²)			
	Open	Shrub	Edge	Forest	Open	Shrub	Edge	Forest	Open	Shrub	Edge	Forest
<i>Q. acutifolia</i>	1.6 b (0.6)	2.9 ne (0.2)	2.0 b (0.3)	4.4 b (0.4)	35.3 ne (0.3)	7.7 ne (1.1)	13.8 ab (1.1)	9.6 c (4.9)	15.1 ab (4.8)	13.5 ne (2.7)	11.7 c (2.3)	9.6 c (0.9)
<i>Q. castanea</i>	1.6 b (0.4)	1.9 ne (0.7)	1.7 b (0.3)	2.8 b (0.8)	20.8 ne (6.9)	7.4 ne (0)	13.1 c (2.3)	12.2 c (4.4)	7.5 ab (1.6)	4.4 ne (1.0)	4.9 c (1.3)	6.8 c (1.5)
<i>D. viscosa</i>	4.0 b (0.3)	3.6 b (0.4)	3.9 b (0.2)	5.1 b (0.5)	15.3 ab (0.0)	13.7 c (0.8)	13.5 c (1.2)	11.7 c (1.5)	103.7 a (28.3)	80.2 ab (11.4)	65.6 ab (10.2)	75.2 ab (8.1)
<i>R. virens</i>	7.7 ab (1.0)	5.7 b (0.7)	13.1 a (1.6)	13.5 a (2.6)	24.9 ab (2.8)	26.5 a (4.4)	20.3 ab (4.6)	14.5 ab (1.7)	80.1 ab (16.2)	43.4 ab (7.2)	109.5 a (17.3)	68.8 ab (14.9)

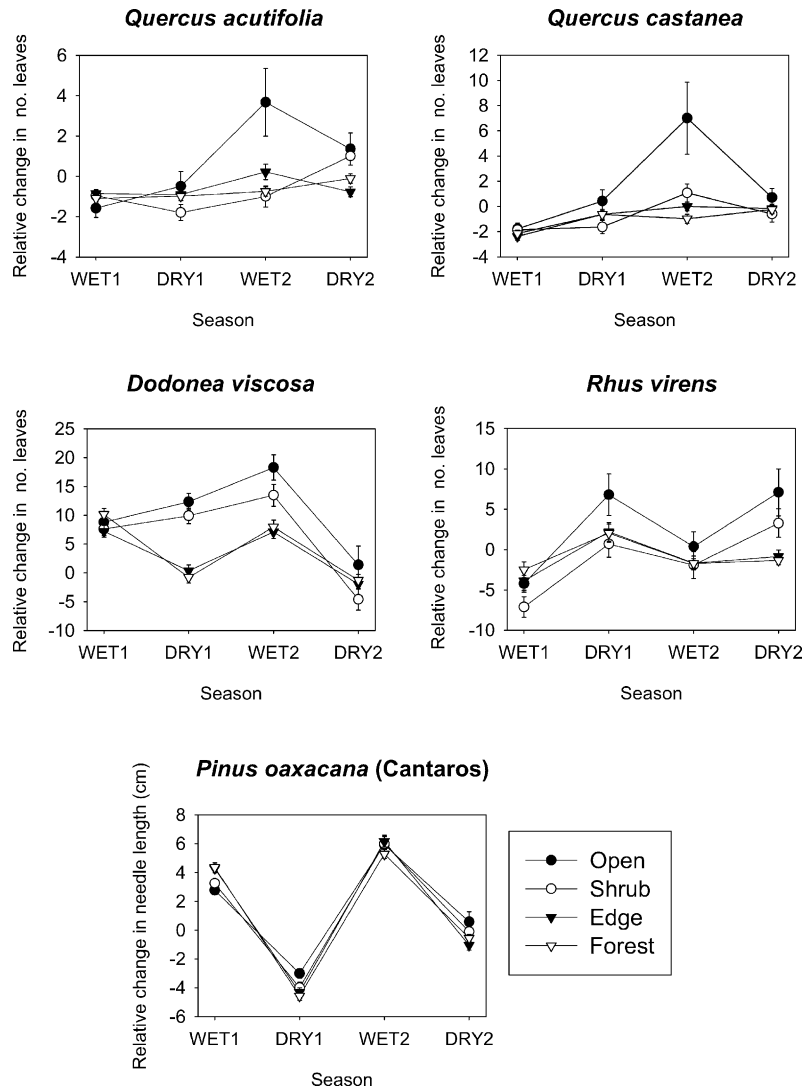


Fig. 3. Mean relative change in leaf number for seedlings growing in four different microsites, by species and season—WET1: 1st wet season (July 1996–November 1996); DRY1: 1st dry season (December 1996–May 1997); WET2: 2nd wet season (June 1997–November 1997); DRY2: 2nd dry season (December 1997–February 1998). For *P. oaxacana*, mean change in leaf length is reported. Scales on each graph vary.

higher leaf number during the wet season, while *R. virens* had the highest leaf number during the dry season (Fig. 3). Oak seedlings growing in the open microsites also had a higher leaf number during the wet season, although the degree of change was significantly less than that recorded for the shrub species. For the pine seedlings, needle length changed strongly in response to season, with length being greatest in the wet season and shortest in the dry season, probably

reflecting patterns of senescence and turnover. All species increased leaf production at the onset of the wet season; however, only *D. viscosa* continued to increase its leaf number throughout the wet season and continuing on into the following dry season, particularly in the open and shrub microsites (Fig. 4). Pine seedlings had needle lengths increasing during both the second wet and dry seasons, with the strongest change in needle length observed for seedlings growing in the

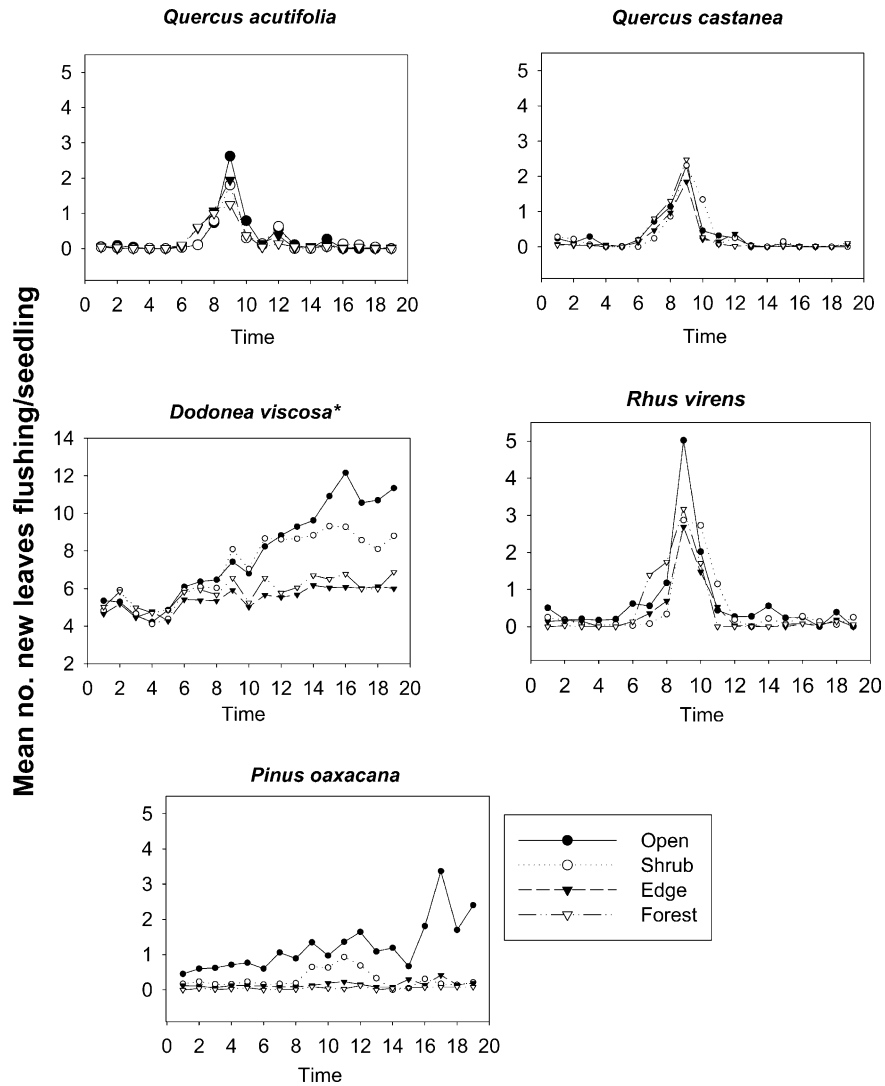


Fig. 4. Mean number of leaves flushing per seedling, by species and for different time periods (1, December 1996; 2, February 1997; 3, February 1997; 4, February 1997; 5, March 1997; 6, April 1997; 7, April 1997; 8, April 1997; 9, May 1997; 11, June 1997; 12, July 1997; 13, August 1997; 14, September 1997; 15, October 1997; 16, November 1997; 17, December 1997; 18, January 1998; 19, February 1998). Scale for *D. viscosa* figure is different.

open microsites. In contrast, the oak seedlings did not continue to produce new leaves after the initial flush early in the wet season. Comparing across species, *D. viscosa* produced more new leaves (average of 14 leaves produced per plant) than all other species (0.3–3.3 new leaves produced) during the study period. The total number of leaves senescing on the seedlings was greatest in the open and shrub microsites com-

pared to the edge and forest microsites; the only exception was recorded for *P. oaxacana* seedlings, which had greater leaf senescence when growing in the edge and forest microsites (data not shown). Leaf senescence generally increased during the dry season for all species, with *D. viscosa* having a significant increase in the rate of leaf senescence during the second dry season.

4.3. Mortality

Comparing mortality rates among species, *Q. castanea* had the highest mortality rate (53%), followed by *Q. acutifolia* (37%) and *P. oaxacana* (35%). *R. virens* and *D. viscosa* had the lowest mortality rates (13 and 3%, respectively). In general, the greatest seedling mortality was recorded during the second year of the study for all species, and mortality was

consistently higher for seedlings growing in the open and shrub microsites compared to the edge and forest microsites (Fig. 5). Comparing among opening types, oak and pine seedlings growing in the large and small openings in the highly fragmented landscape had greater mortality than in the reference landscape, although these trends were not significant (Fig. 6). In general, differences in mortality rates between both microsites and opening types were more pronounced

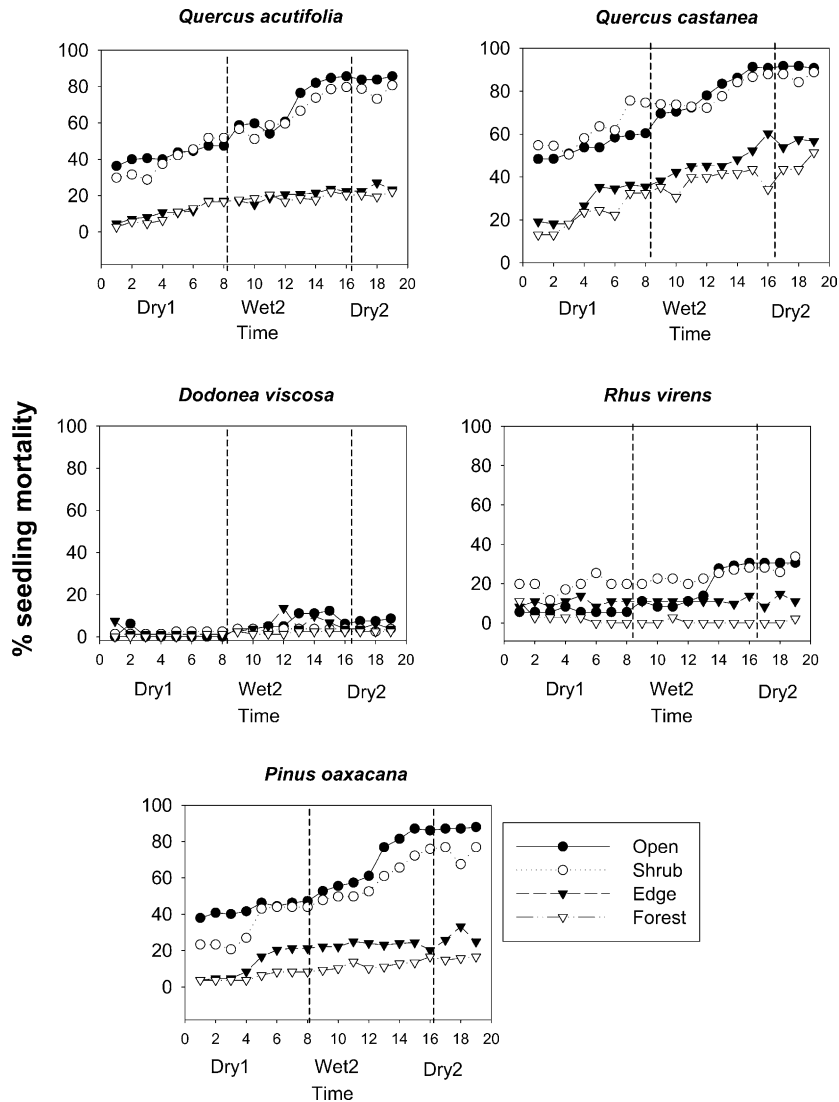


Fig. 5. Percent seedling mortality by species for different time periods (1, December 1996; 2, February 1997; 3, February 1997; 4, February 1997; 5, March 1997; 6, April 1997; 7, April 1997; 8, April 1997; 9, May 1997; 11, June 1997; 12, July 1997; 13, August 1997; 14, September 1997; 15, October 1997; 16, November 1997; 17, December 1997; 18, January 1998; 19, February 1998).

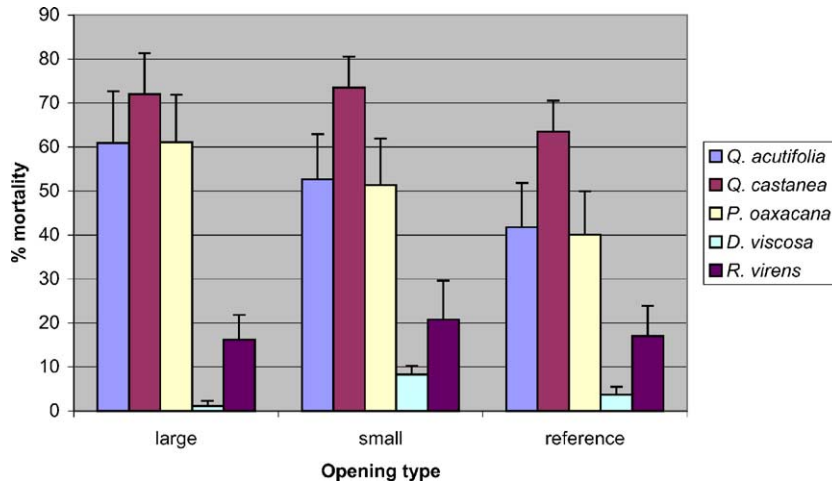


Fig. 6. Mean (\pm S.E.) percent seedling mortality for seedlings of five species, comparing across different opening sizes (large, small, and reference), 2 years following transplanting to the field.

for the oak and pine species compared to the shrub species.

4.4. Pre-dawn water potential

The physiological response of the seedlings to soil moisture availability as reflected by ψ_{pd} varied significantly among species. *Q. acutifolia* and *Q. castanea* consistently exhibited the lowest ψ_{pd} (−3.89 and −3.75 MPa, respectively), followed by *R. virens* and *D. viscosa* (−3.14 and −2.85 MPa, respectively) (Table 5). *P. oaxacana* maintained the highest ψ_{pd} of all the species (−2.21 MPa).

When comparing across microsites, data from the open and shrub microsites were pooled (‘open’) and data from the edge and forest microsites (‘forest’)

were pooled because high mortality rates resulted in low total sample sizes. Only *D. viscosa* and *R. virens* had significantly different ψ_{pd} between the two categories of pooled microsites, with seedlings of both species having the lowest ψ_{pd} in forest microsites (−3.50 and −3.36 MPa, respectively) compared to open microsites (−2.37 and −2.93 MPa, respectively) (Table 5). For the oaks and pines, no significant differences in ψ_{pd} were recorded when comparing between microsites.

5. Discussion

The results of our study suggest that differences in seedling growth and physiological characteristics strongly influence establishment success, and that regeneration processes are further mediated by microclimate change across edge environments and annual climatic fluctuations, and to a lesser extent, by the degree of habitat fragmentation in the landscape. Although the relatively short 2-year time frame of the study limits our capacity to make long-term projections about seedling survival and successional processes, our results do reveal patterns about differences among species during the critical establishment phase. The role of individual plant species, the edge environment (microsite variability), and landscape characteristics (degree of habitat fragmentation)

Table 5
Means (\pm S.E.) for pre-dawn leaf water potentials (ψ_{pd}) for seedlings growing in open and forest microsites, and for all seedlings pooled

Species	ψ_{pd}		
	Microsites pooled	Open microsite	Forest microsite
<i>Q. acutifolia</i>	−4.0 (0.1)	−4.0 (0.2)	−3.9 (0.2)
<i>Q. castanea</i>	−3.8 (0.2)	−3.8 (0.5)	−3.7 (0.2)
<i>D. viscosa</i>	−2.9 (0.1)	−2.4 (0.1)	−3.5 (0.1)
<i>P. oaxacana</i>	−2.1 (0.1)	−2.2 (0.1)	−2.1 (0.1)
<i>R. virens</i>	−3.1 (0.1)	−2.9 (0.2)	−3.4 (0.2)

in controlling regeneration dynamics in these highland tropical landscapes are discussed below.

5.1. Plant species' growth and physiological characteristics

Differences in growth traits and physiological responses exhibited by the species examined in this study appear to be strongly related to species' life form and successional sere. In particular, the low total seedling biomass (1.1–1.9 g) and exceptionally high mortality rates (20 to >80%) of the oaks and pines contrasted sharply with the high total seedling biomass (5.2–8.6 g) and relatively low mortality rates (3–13%) of the shrubs. The low relative height growth and total seedling biomass of the two oak species, *Q. acutifolia* and *Q. castanea*, agrees with other studies suggesting that oaks generally have conservative growth strategies (Gudmunds and Barbour, 1987; Lloyd and Waldrop, 1992; Chaar et al., 1997). Conservative growth strategies (i.e., slow relative growth rates, greater allocation to belowground structures, longer leaf longevity, more resistant leaf structures) may be important adaptations for tolerating stress and providing a long-term competitive advantage when resources are scarce, but constraining growth when resources are more abundant (Grime, 1977; Bazzaz, 1979; Lambers and Poorter, 1992). Shoot die-back, another important adaptive response of oak species to unfavorable conditions that enables rapid reduction in leaf area followed by resprouting once conditions become more favorable (Crow, 1992; Crunkilton et al., 1992; Collet et al., 1997; Chaar et al., 1997), was also especially pronounced in the two oak species. *P. oaxacana* seedlings were distinguished by their significantly lower height growth when growing in the forest understory compared to more open environments, which agrees with the light-demanding and highly drought-tolerant growth strategy common to the genus *Pinus* (Vance and Zaerr, 1991; Pallardy et al., 1995). The relatively rapid height growth and high biomass observed for the two shrub species, *D. viscosa* and *R. virens*, indicate an opportunistic growth strategy characteristic of early successional species (i.e., fast relative growth rates, greater allocation to productive tissues, and faster leaf turnover rates; Grime, 1977; Bazzaz, 1979; Lambers and Poorter, 1992). *D. viscosa*'s faster growth and higher specific leaf area

and total leaf area suggested that it was the most highly opportunistic of the two shrub species.

Pre-dawn soil water potential, which integrates spatial heterogeneity in soil moisture available to a plant across its entire root system (Ritchie and Hinckley, 1975; Fahey and Young, 1984; Mitchell et al., 1993), appeared to explain some of the differences observed in growth response of the different species. The extremely low ψ_{pd} recorded for *Q. acutifolia* and *Q. castanea* seedlings (−4.0 and −3.8 MPa, respectively) suggests that high mortality of oak seedlings may be related to moisture stress. Although certain xeric oak species were found to exhibit low ψ_{pd} and high capacity to sustain stomatal opening under drought stress (Parker et al., 1982), poor stomatal control (Abrams, 1990) combined with high vulnerability to water stress-induced xylem embolism (Cochard and Tyree, 1990; Shumway et al., 1993; Davis et al., 1998) may limit the establishment of shallow-rooted seedlings under conditions of high water stress (Meentemeyer et al., 2001). In contrast to the oaks, the shrub species maintained higher average ψ_{pd} (−2.9 MPa), indicating more favorable seedling water status. The pine seedlings consistently maintained the highest ψ_{pd} of all the species (−2.1 MPa), likely associated with conservative water use patterns typical of many conifer species in which desiccation is avoided by minimizing transpiration during drought (DeLucia and Schlesinger, 1991; Fredericksen et al., 1993; Royce and Barbour, 2001). Similarly, conifers have also been shown to be more sensitive to vapor pressure deficits than broad-leaved species, as reflected by rapidly declining stomatal conductance under moisture stress (Marshall and Waring, 1984). Although photosynthesis is reduced when ψ_{pd} increases in response to drought due to stomatal closure, total productivity can still be relatively high due to year-round photosynthesis (Schoettle and Fahey, 1994; Waring and Franklin, 1979). Drought effects on pine seedlings may therefore have been less severe than on oak seedlings due to their capacity to control water loss by maintaining higher ψ_{pd} .

Varying phenological responses among species to drought may also help explain their different growth patterns observed in this study. Although leaf production was highest for all species when growing in high light environments, as found in other studies (Quintana-Ascencio et al., 1992; Nilsson and Hällgren,

1993; Thadani and Ashton, 1995; Negi et al., 1996), exceptionally high leaf production and turnover rates in *D. viscosa* contrasted sharply with the slower rates in the other species. Production of new leaves by *D. viscosa* seedlings was particularly pronounced during the extreme drought, during which *D. viscosa* produced an average of 14 new leaves per seedling compared to only 0.3–3.3 new leaves per seedling produced by the oaks and *R. virens*. Thus, high rates of leaf senescence and turnover may be a physiological adaptation enabling *D. viscosa* to quickly drop its leaves in order to avoid moisture stress, thereby minimizing water loss from transpiring surfaces, and to flush new leaves once conditions became favorable again (Stone and Bacon, 1995; Correia and Martins-Loução, 1997; Arndt et al., 2001). Like *D. viscosa*, pine seedlings growing in the forest edge and understory microsites also had high leaf senescence. Leaf shedding in response to moisture stress has also been documented for *P. radiata* (Raison et al., 1992). However, unlike the shrub species, leaf production and turnover in pine seedlings was also low. This may be a result of the pine's light-demanding physiology and inability to maintain a favorable carbon balance in shady conditions. Leaf shedding in response to drought stress appears to be much less common in oak species (Pallardy and Rhoads, 1993), while other traits such as production of xeromorphic leaf structures and high leaf longevity may be more important for tolerating environmental stress (Chabot and Hicks, 1982; Lambers and Poorter, 1992; Salleo et al., 1997).

The two major life forms represented by the species included in this study—trees and shrubs—appear to be a determining factor affecting the observed differences among species in their growth and physiological responses. Trees, even at the early seedling stage, tend to allocate greater proportions of photosynthate to woody structures and, in turn, have slower growth rates and smaller leaf area ratios (total leaf area/plant dry weight) than shrubs or herbaceous plants (Cornelissen et al., 1996), as reported in our study. In general, evergreens have greater allocation to non-photosynthetic leaf structures and lower relative growth rates compared to deciduous species (Cornelissen et al., 1996); however, these findings were not supported by our results, possibly due to the longer leaf life span in tropical oaks, which may cause their biomass alloca-

tion patterns to more closely resemble that of evergreen conifers. Although trees were found to obtain water from deeper sources than grasses and shrubs and therefore maintain coexistence through effective partitioning of resources (Dodd et al., 1998), young oak seedlings (<2 years old) were reported to compete directly with grasses for the same water source (Weltzin and McPherson, 1997). Thus, differing physiologies among tree and shrub life forms, combined with changing resource use patterns associated with life history stage, may further explain differences among species' responses to environmental stress observed in our study.

Although *Q. castanea* was predicted to be the more drought tolerant of the two oak species based on its smaller leaf size and slower growth rates (Pallardy and Rhoads, 1993; Long and Jones, 1996), the greater survival rate observed for *Q. acutifolia* contradicted these expectations. Both species allocated greater biomass to roots than to aboveground plant components, which is consistent with a drought adaptive strategy of xeric oak species (Matsuda et al., 1989; Abrams, 1994; Long and Jones, 1996). However, higher relative growth rates of *Q. acutifolia* enabled the establishment of a greater total root mass and root length, which likely enhanced its capacity to access moisture during the second year drought. Further, low leaf plasticity in response to shading by *Q. castanea* compared to *Q. acutifolia*—in which leaf size did not increase in the former but did in the latter—may have prevented *Q. castanea* from maintaining a positive carbon balance in the forest and edge environments. Pallardy and Rhoads (1993) reported that the highly drought-tolerant oak species, *Q. stellata*, was least effective in curtailing water loss after stomatal closure compared to the less drought-tolerant species *Q. alba*. Growth differences between xeric and hydric oak species were found to be greatest for young seedlings compared to larger and older seedlings (Long and Jones, 1996), while oak seedlings in semi-arid Mediterranean climates often experience exceptionally high mortality rates during the first dry season (Rey Benayas, 1998). Thus, the extremely slow growth rates and high costs of production of leaf and root structures in highly xeric oak species native to these tropical highlands may reduce the capacity of young oak seedlings to withstand severe drought during the initial period of seedling establishment.

5.2. Influence of microclimate variation across edge environments on seedling response

Edges between forest patches and openings in fragmented landscapes may exert significant controls over seedling growth and survival patterns on a landscape scale, due to spatial and temporal changes in microclimate that occur across edge environments (Chen et al., 1992, 1993). The species examined in our study responded differently to microsite conditions associated with position along the edge gradient. In particular, oaks and pines were more sensitive to microclimate differences than the shrub species, as indicated by the degree of variability in the response variables measured for seedlings growing in different edge microsites. Both total seedling biomass and mortality rate of the oak seedlings increased progressively from the forest into the open microsites and were most pronounced during the drought. Pine seedlings had similar trends in mortality and biomass as the oaks, with the exception of the high biomass recorded for pine seedlings growing in the open microsites. In contrast, biomass and mortality rates for the shrub seedlings did not vary significantly across the edge gradient or in response to the severe drought, suggesting low sensitivity to temporal and spatial changes in microclimatic conditions created by the edges.

The varying patterns in seedling survival and biomass between the tree and shrub species may be explained by their differing capacities to access limited soil moisture. Edge environments at the study site were characterized by a strong microclimate gradient in which soil moisture in the surface horizon increased from the open into the forest understory (ranging from 10.8 to 40.1 g m⁻³ versus 16.8 to 54.7 g m⁻³, respectively), with corresponding decreases in light and temperature (Asbjornsen et al., in press). Other studies have shown that soil moisture generally increases at greater depths in open environments, due to the absence of water uptake and evapotranspiration by deep-rooted trees (Minckler et al., 1973; Liechty et al., 1992; Bréda et al., 1995; Veenendaal et al., 1995; Breashears et al., 1997). Although both oaks (Abrams, 1990) and pines (Reich et al., 1992; Caspersen and Kobe, 2001) are considered to be among the most drought-tolerant forest species, the relatively small and shallow root systems of the oak and pine seedlings in our study would have confined water uptake to the

upper soil horizon where soil moisture was especially low in the open and shrub microsites. These findings agree with studies of oak species in temperate savanna ecosystems suggesting that during the first 2–3 years of seedling establishment, seedlings are incapable of accessing deeper water sources (Pase, 1969; Brown and Archer, 1990; Weltzin and McPherson, 1997). When comparing Mediterranean oak (*Quercus ilex*) and pine (*Pinus halepensis*) seedling responses to shading, Broncano et al. (1998) found that the pine consistently outperformed the oak and had a wider regeneration niche. Similarly, our results suggest that threshold levels in the amount of moisture required for successful pine and oak regeneration may be slightly higher for the oaks compared to the pines, as reflected by the higher mortality rates of the former, although this threshold was apparently surpassed for both species during the extreme drought year. Similarly, in contrast, the faster growth rates and correspondingly greater root biomass and deeper rooting habit of the shrub species likely enabled them to access deeper soil horizons, thereby contributing to their generally higher survival and biomass accumulation across all microsite positions. Interestingly, the few oak and pine seedlings that were able to survive in the open environment produced more total biomass than seedlings of the same species growing in the forest and edge microsites, which appears to corroborate the earlier notion that surviving seedlings had developed sufficiently deep root systems to access deeper water supplies and thus benefit from higher light availability in more open environments. The extreme case was observed for pine seedlings growing in open environments that attained an average biomass of 8.1 g, which exceeded the biomass of the shrub seedlings. Similar patterns of high mortality in open areas combined with greater biomass of the surviving plants have been reported elsewhere (Barton, 1993; Negi et al., 1996; Buckley et al., 1998).

Differences in species' pre-dawn soil water potential for seedlings growing in different microsites across the edge gradient provide a physiological explanation of the differences observed in growth response. The shrub species demonstrated the greatest change in ψ_{pd} of seedlings growing in the different microsites, with significantly higher values recorded for seedlings growing in the open microsites (−2.4 MPa) compared to the forest microsites (−3.5 MPa). This difference

was likely due to limited water availability at lower soil depths in the forest environment as a result of higher rates of water uptake and evapotranspiration by mature trees (Bahari et al., 1985; Crunkilton et al., 1992; Conrad et al., 1997). Further, the relatively high plant biomass and surface area produced by shrub seedlings growing in the forest understory in our study may have exacerbated the effects of moisture stress by greatly increasing transpiration demand. This suggests that high relative growth rates may be a disadvantage under more competitive and resource limited forest understory environments (Lambers and Poorter, 1992), especially during periods of drought. Although the lower ψ_{pd} did not immediately translate into higher mortality rates for the shrub seedlings in our study, frequent moisture stress may prohibit shrubs from persisting in the forest understory in the long term. Drought stress experienced by the shrub seedlings growing in the forest and edge microsites may have been partly alleviated by leaf shedding and high leaf turnover, enhancing survivorship of the seedlings at least in the short term.

The similarly low ψ_{pd} in oak seedlings growing in both the open and forest microsites combined with the greater mortality in the open microsites suggests that, for the oak seedlings, other factors besides soil moisture availability (e.g., high atmospheric vapor pressure deficits (Sala and Tenhunen, 1994; Burton and Bazzaz, 1995) or lack of stomatal control (Meentemeyer et al., 2001)) may have contributed to increased physiological stress in the open environment. The relatively high ψ_{pd} maintained by the pine seedlings growing in both open and forest microsites, reflecting their conservative water use physiology (see above), may have contributed to their greater survival rates compared to the oaks. Neither the pine nor oak seedlings appeared to have the capacity to reduce drought stress by excessive leaf shedding and high leaf turnover rates, agreeing with patterns of lower physiological plasticity common to later successional species.

The greater survival of oak and pine seedlings in the forest understory and edge environments in our study also suggests that mature trees and shrubs may have a facilitative effect on seedling regeneration, as observed in other studies (De Steven, 1991; Gill and Marks, 1991; Callaway, 1992; Barton, 1993; Owens et al., 1995; Raffaele and Veblen, 1998).

Although high evapotranspiration rates by larger, deeply rooted trees and shrubs may deplete soil moisture and enhance moisture stress in the understory, shading by the overstory canopy may also ameliorate microclimate conditions by reducing direct sunlight, moderating fluctuations in ground and air temperature, and protecting against surface soil moisture loss (Belsky et al., 1989, 1993; Joffre and Rambal, 1993; Breashears et al., 1997). These ameliorative effects of trees on the understory environment and plant growth may be especially enhanced in more dry environments (Ong and Leakey, 1999). Similarly, trees have been found to either facilitate or inhibit oak seedling establishment and growth depending on the climatic regime: in moist environments oak seedling mortality is generally greater when growing in the forest understory than in the open (Lorimer et al., 1994), while the reverse is often the case in dry environments (Callaway and D'Antonio, 1991; Callaway, 1992; Pugnaire and Haase, 1996; Negi et al., 1996). Our results suggest that in this seasonally dry tropical highland ecosystem, the survival of seedlings of late-successional oak species (and to some extent mid-successional pine species) may be favored by the proximity of an overstory tree canopy, with the forest matrix providing an important buffering function by ameliorating environmental conditions through enhanced surface soil moisture (Asbjornsen et al., *in press*). However, since total seedling biomass was greater for seedlings surviving in open and edge environments compared to the forest understory, interactions between facilitation processes and long-term seedling growth and forest regeneration require further research.

5.3. Influence of habitat fragmentation on seedling response

In this study, differences in the degree of habitat fragmentation between the two landscapes examined, both in terms of matrix environment (predominantly forest under low fragmentation versus predominantly open under high fragmentation) and opening size (<0.1 ha versus >1.0 ha), appeared to have relatively less influence on seedling response compared to edge effects. Although a general trend was observed in which all species exhibited slightly lower mortality in the less fragmented landscape (reference openings)

compared to the more highly fragmented landscape (small and large openings), and oak seedlings also produced greater biomass in the less fragmented landscape, these differences were much less pronounced than those occurring between the different edge microsites. This indicates that small scale differences in microclimate occurring across edge environments may exert greater control over regeneration dynamics than the more broad landscape scale characteristics resulting from habitat fragmentation and vegetation cover changes. However, it is also possible that the parameters measured in this study may not have been sensitive to large landscape scale processes, or that greater replication is required in order to capture these patterns. Further, since oak forests are disturbance dependent ecosystems with seedling growth often being greatest in open or shrub areas or forest gaps (Quintana-Ascencio et al., 1992), the limiting factor for regeneration with increasing habitat fragmentation due to forest cover removal may be dispersal distance for acorns or lack of effective vectors.

6. Conclusions

These results of this study suggest that synergistic interactions between microclimate conditions and drought across edge environments may strongly control patterns of regeneration in fragmented landscape by constraining the successful establishment of oak and pine species and favoring more opportunistic, faster-growing shrub species. Further, a key factor determining successful establishment of oak and pine seedlings during the initial regeneration phase is whether seedlings encounter favorable microclimate conditions to enable them to develop a sufficiently deep and extensive root system capable of accessing available water from lower soil depths, especially in more open environments. Thus, synergistic interactions between extreme disturbance events and fragmentation processes may directly influence the rate and direction of regeneration pathways. The occurrence of a series of 3–4 relatively wet years are probably needed to provide a window of opportunity for oak and pine seedlings to establish, especially in the more harsh environments that prevail in open clearings and highly fragmented landscapes. Although oak seedlings may survive in the forest understory for

a period of time, long-term regeneration success likely requires high light conditions found in more open environments (Quintana-Ascencio et al., 1992; Espelta et al., 1995; Abrams, 1996). Our study further suggests that oak and pine regeneration processes may be facilitated (and the regeneration window widened) in edge environments where the presence of mature trees and shrubs may ameliorate site conditions by providing shade, reducing evaporation, and improving surface soil moisture availability.

In these highly fragmented landscapes where forest cover has been removed, shrubs appear to have a competitive advantage over trees since they can more rapidly exploit available resources during sporadic periods of favorable growing conditions. Further, the severely altered environmental conditions may lead to development of alternative ecosystem states, within which later successional species are unable to reestablish for extensive periods of time (Niering and Egler, 1955; Putz and Canham, 1992; Sarmiento, 1997). The shift towards greater establishment of shrubs in fragmented landscapes in the highlands of southern Mexico, especially under unfavorable climatic periods, may either preclude oak regeneration completely or result in extremely slow regeneration rates.

Since drought is a reoccurring phenomenon in these landscapes, management strategies aimed at facilitating regeneration of mature oak forests must include the influence of these decadal scale disturbances on the composition and structure of successional plant communities in these tropical highland landscapes. Specific management interventions can be designed to enhance the inherent resilience of these highland tropical oak ecosystems and ensure the maintenance of the ecological functions. In particular, transplanting oak and pine seedlings with a well-developed root system into edge and open environments may enable the system to overcome thresholds to natural regeneration processes caused by synergistic interactions between habitat fragmentation and periodic drought in these landscapes. Although not directly addressed in our study, the role of both anthropogenic and naturally occurring fire in maintaining oak forests in these landscapes deserves greater attention, especially since fire is a major disturbance factor in most oak ecosystems, including montane oak–pine forests in Mexico (Rzedowski, 1978; Gonzalez-Espinosa et al., 1991;

Park, 2001), and its suppression has been implicated as a potential cause of reduced oak regeneration (Johnson et al., 2002).

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References

- Abrams, M.D., 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiol.* 7, 227–238.
- Abrams, M.D., 1994. Genotypic and phenotypic variation as stress adaptations in temperate tree species: a review of several case studies. *Tree Physiol.* 14, 833–842.
- Abrams, M.D., 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. *Ann. Sci. For.* 53 (2–3), 487–512.
- Arndt, S.K., Clifford, S.C., Wanek, W., Jones, H.G., Popp, M., 2001. Physiological and morphological adaptations of the fruit tree *Ziziphus rotundifolia* in response to progressive drought stress. *Tree Physiol.* 21, 705–715.
- Asbjornsen, H., Ashton, M.A., Vogt, D.J., Palacios, S., in press. Effects of habitat fragmentation on the buffering capacity of edge environments in a seasonally dry tropical oak forest ecosystem in Oaxaca, Mexico. *Agric. Ecosyst. Environ.*
- Bahari, Z.A., Pallardy, S.G., Parker, W.C., 1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak–hickory forests in Central Missouri. *For. Sci.* 31 (3), 557–569.
- Barton, A.M., 1993. Factors controlling plant distributions: drought, competition, and fire in montane pines in Arizona. *Ecol. Monogr.* 63 (4), 367–397.
- Bazzaz, F.A., 1979. The physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.* 10, 351–371.
- Belsky, A.J., Amundson, A.G., Duxbury, J.M., Riha, S.J., Ali, A.R., Mwonga, S.M., 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *J. Appl. Ecol.* 26, 1005–1024.
- Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M., Ali, A.R., 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *J. Ecol.* 30 (1), 143–155.
- Benitez-Malvido, J., 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conserv. Biol.* 12 (2), 380–389.
- Breashears, D.D., Rich, P.M., Barnes, F.J., Campbell, K., 1997. Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecol. Appl.* 7, 1201–1215.
- Bréda, N., Granier, A., Aussenac, G., 1995. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). *Tree Physiol.* 15, 295–306.
- Broncano, M.J., Riba, M., Retana, J., 1998. Seed germination and seedling performance of two Mediterranean tree species, holm oak (*Quercus ilex* L.) and Aleppo pine (*Pinus halepensis* Mill.): a multifactor experimental approach. *Plant Ecol.* 138, 17–26.
- Brown, J.R., Archer, S.R., 1990. Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. *Oikos* 57, 366–374.
- Buckley, D.S., Sharik, T.L., Isebrands, J.G., 1998. Regeneration of northern red oak: positive and negative effects of competitor removal. *Ecology* 79 (1), 65–78.
- Bunnell, F.L., Huggard, D.J., 1999. Biodiversity across spatial and temporal scales: problems and opportunities. *For. Ecol. Manage.* 115, 113–126.
- Burke, D.M., Nol, E., 1998. Edge and fragment size effects on the vegetation of deciduous forest in Ontario, Canada. *Nat. Areas J.* 18 (1), 45–53.
- Burton, P.J., Bazzaz, F.A., 1995. Ecophysiological responses of tree seedlings invading different patches of old-field vegetation. *J. Ecol.* 83, 99–112.
- Caldwell, M.M., Richards, J.H., 1989. Hydraulic lift water efflux from upper roots improves effectiveness of water up-take by deep roots. *Oecologia* 79, 1–5.
- Callaway, R.M., 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73 (6), 2118–2128.
- Callaway, R.M., D'Antonio, C.M., 1991. Shrub facilitation of coast live oak establishment in central California. *Madrono* 38, 158–169.
- Caspersen, J.P., Kobe, R.K., 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. *Oikos* 92, 160–168.

- Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2002. Use of shrubs as nurse plants: a new technique for reforestation in Mediterranean mountains. *Restor. Ecol.* 10 (2), 297–305.
- Chaar, H., Colin, F., Collet, C., 1997. Effects of environmental factors on the shoot development of *Quercus petraea* seedlings: a methodological approach. *For. Ecol. Manage.* 97, 119–131.
- Chabot, B.F., Hicks, D.J., 1982. The ecology of leaf life-spans. *Annu. Rev. Ecol. Syst.* 13, 229–259.
- Chen, J., Franklin, J.F., Spies, T.A., 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecol. Appl.* 2 (4), 387–396.
- Chen, J., Franklin, J.F., Spies, T.A., 1993. Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agric. For. Meteorol.* 63, 219–237.
- Cochard, H., Tyree, M.T., 1990. Xylem dysfunction in *Quercus*: vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiol.* 6, 393–407.
- Collet, C., Colin, F., Bernier, F., 1997. Height growth, shoot elongation and branch development of young *Quercus petraea* grown under different levels of resource availability. *Ann. Sci. For. (Paris)* 54, 65–81.
- Conrad, S.G., Sparks, S.R., Regelbrugge, J.C., 1997. Comparative plant water relations and soil water depletion patterns of three seral shrub species on forest sites in southwestern Oregon. *For. Sci.* 43 (3), 336–347.
- Cornelissen, J.H.C., Diez, P.C., Hund, R., 1996. Seedling growth, allocation and leaf attributes in a wide range of woody species and types. *J. Ecol.* 84, 755–765.
- Correia, P.J., Martins-Loução, M.A., 1997. Leaf nutrient variation in mature carob (*Ceratonia siliqua*) trees in response to irrigation and fertilization. *Tree Physiol.* 17, 813–819.
- Crow, T.R., 1992. Population dynamics and growth patterns for a cohort of northern red oak (*Quercus rubra*) seedlings. *Oecologia* 91 (2), 192–200.
- Crunkilton, D.D., Pallardy, S.G., Garrett, H.E., 1992. Water relations and gas exchange of northern red oak seedlings planted in a central Missouri clearcut and shelterwood. *For. Ecol. Manage.* 53, 117–129.
- Davis, M.A., Wrage, K.J., Reich, P.B., 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *J. Ecol.* 86, 652–661.
- Dawson, T.E., 1993. Hydraulic lift and water use by plants: implications for water balance, performance, and plant–plant interactions. *Oecologia (Berlin)* 95, 565–574.
- De Steven, D., 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. *Ecology* 72, 1076–1088.
- DeLucia, E.H., Schlesinger, W.H., 1991. Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. *Ecology* 72 (1), 51–58.
- Doak, D.F., Marino, P.C., Kareiva, P.M., 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theor. Popul. Biol.* 41, 315–336.
- Dodd, M.B., Lauenroth, W.K., Welker, J.M., 1998. Differential water resource use by herbaceous and woody plant life-forms in a shortgrass steppe community. *Oecologia* 117, 504–512.
- Espelta, J.M., Riba, M., Retana, J., 1995. Patterns of seedling recruitment in West-Mediterranean *Quercus ilex* forests influenced by canopy development. *J. Veg. Sci.* 6, 465–496.
- Euskirchen, E.S., Chen, J., Bi, R., 2001. Effects of edges on plant communities in a managed landscape in northern Wisconsin. *For. Ecol. Manage.* 148, 93–108.
- Fahey, T.J., Young, D.R., 1984. Soil and xylem water potential and soil water content in contrasting *Pinus contorta* ecosystems, southeastern Wyoming, USA. *Oecologia (Berlin)* 61, 351–436.
- Ferreira, L.V., Laurance, W.F., 1997. Effects of forest fragmentation on mortality and damage of selected trees in Central Amazonia. *Conserv. Biol.* 11 (3), 797–801.
- Ferrusquia-Villafranca, I., 1976. Estudios Geologico-Paleontologicos en la Region Mixteca, PT. 1. Geologica del area Tamazulapan-Teposcolula-Yanhuitlan, Mixteca Alta, Estado de Oaxaca, Mexico. Universidad Nacional Autónoma de Mexico Instituto de Geología.
- Forman, R.T.T., Godron, M., 1986. *Landscape Ecology*. Wiley, New York.
- Fredericksen, T.S., Shepard, M.Z., Smith, D.W., Seiler, J.R., Kreh, R.E., 1993. Interference interactions in experimental pine-hardwood stands. *Can. J. For. Res.* 23, 2032–2043.
- García-Mendoza, A., Cruz, F.P., 1993. A new species of *Agave* (*Agavaceae* subgenus *Agave*) from Oaxaca and Chiapas, Mexico. *SIDA Contrib. Bot.* 15 (4), 565–568.
- Gelhausen, S.M., Schwartz, M.W., Augspurger, C.K., 2000. Vegetation and microclimate edge effects in two mixed-mesophytic forest fragments. *Plant Ecol.* 147, 21–35.
- Gill, D.S., Marks, P.L., 1991. Tree and shrub seedling colonization of old fields in Central New York. *Ecol. Monogr.* 61, 183–205.
- Gonzalez-Espinosa, M., Quintana-Ascencio, P.F., Ramirez-Marcial, N., Gaytan-Guzman, P., 1991. Secondary succession in disturbed *Pinus-Quercus* forests in the highlands of Chiapas, Mexico. *J. Veg. Sci.* 2, 351–360.
- Gordon, D.R., Welker, J.M., Menke, J.W., Rice, K.J., 1989. Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. *Oecologia (Berlin)* 79, 533–541.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. Nat.* 111, 1169–1194.
- Gudmunds, K.N., Barbour, M.G., 1987. Mixed evergreen forest stands in the northern Sierra Nevada. USFS General Technical Report PSW-100, pp. 32–37.
- Joffre, R., Rambal, S., 1988. Soil water improvement by trees in the rangelands of southern Spain. *Acta Oecol.* 9 (4), 405–422.
- Joffre, R., Rambal, S., 1993. How tree cover influences the water balance of Mediterranean rangelands? *Ecology* 74 (2), 570–582.
- Johnson, P.S., Shifley, S.R., Rogers, R., 2002. *The Ecology and Silviculture of Oaks*. CABI Publishing, New York.
- Lambers, H., Poorter, H., 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Adv. Ecol. Res.* 23, 187–261.
- Laurance, W.F., 2000. Do edge effects occur over large spatial scales? *Trees* 15 (4), 134–135.
- Leuschner, C., 2000. Are high elevations in tropical mountains arid environments for plants? *Ecology* 81 (5), 1425–1436.

- Liechty, H.O., Holmes, M.J., Reed, D.D., Mroz, G.D., 1992. Changes in microclimate after stand conversion in two northern hardwood stands. *For. Ecol. Manage.* 50, 252–264.
- Lloyd, T., Waldrop, T., 1992. Relative growth of oaks and pines in natural mixtures on intermediate to xeric Piedmont sites. In: *Proceedings of the Symposium on Oak Regeneration: Serious Problems, Practical Recommendations*, Knoxville, Tennessee, September 8–10. USDA-FS General Technical Report SE-84, pp. 40–53.
- Long, T.J., Jones, R.H., 1996. Seedling growth strategies and seed size effects in fourteen oak species native to different soil moisture habitats. *Trees (Berlin)* 11, 1–8.
- Lorimer, C.G., Chapman, J.W., Lambert, W.D., 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* 82, 227–237.
- Marshall, J.D., Waring, R.H., 1984. Conifers and broadleaf species: stomatal sensitivity differs in western Oregon. *Can. J. For. Res.* 14, 905–908.
- Martínez-Garza, C., González-Montagut, R., 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. *Plant Ecol.* 145, 255–265.
- Matlack, G.R., 1994. Vegetation dynamics of the forest edge—trends in space and successional time. *J. Ecol.* 82, 113–123.
- Matsuda, K., McBride, J.R., Kimura, M., 1989. Seedling growth form in oaks. *Ann. Bot.* 64, 439–446.
- Meentemeyer, R.K., Moody, A., Franklin, J., 2001. Landscape-scale patterns of shrub-species abundance in California chaparral. *Plant Ecol.* 156, 19–41.
- Minckler, L.S., Woerheide, J.D., Schlesinger, R.S., 1973. Light, soil moisture, and tree reproduction in hardwood forest openings. US Forest Service Research Paper NC-89, p. 6.
- Mitchell, R.J., Zutter, B.R., Green, T.H., Perry, M.A., Gjerstad, D.H., Glover, G.R., 1993. Spatial and temporal variation in competitive effects on soil moisture and pine response. *Ecol. Appl.* 3 (1), 167–174.
- Negi, A.S., Negi, G.C.S., Singh, S.P., 1996. Establishment and growth of *Quercus floribunda* seedlings after a mast year. *J. Veg. Sci.* 7, 559–564.
- Niering, W.A., Egler, F.E., 1955. A shrub community of *Viburnum lentago*, stable for twenty-five years. *Ecology* 36, 356–360.
- Nilsson, U., Hällgren, J., 1993. Changes in growth allocation owing to competition for light in young fertilized Norway spruce trees. *For. Ecol. Manage.* 62, 157–172.
- Nixon, K.C., 1993. The genus *Quercus* in Mexico. In: Ramamoorthy, T.P., Bye, R., Lot, A., Fa, J. (Eds.), *Biological Diversity of Mexico: Origins and Distribution*. Oxford University Press, New York, pp. 447–458.
- Ong, C.K., Leakey, R.R.B., 1999. Why tree–crop interactions in agroforestry appear at odds with tree–grass interactions in tropical savannahs. *Agrofor. Syst.* 45, 109–129.
- Owens, M.K., Wallace, R.B., Archer, S.R., 1995. Landscape and microsite influences on shrub recruitment in a disturbed semi-arid *Quercus–Juniperus* woodland. *Oikos* 74, 493–502.
- Páez, S.A., Marco, D.E., 2000. Seedling habitat structure in dry Chaco forest (Argentina). *J. Arid Environ.* 46, 57–68.
- Pallardy, S.G., Rhoads, J.L., 1993. Morphological adaptations to drought in seedlings of deciduous angiosperms. *Can. J. For. Res.* 23, 1766–1774.
- Pallardy, S.G., Cermák, J., Ewers, F.W., Kaufmann, M.R., Parker, W.C., Sperry, J.S., 1995. Water transport dynamics in trees and stands. In: Smith, W.K., Hinckley, T.M. (Eds.), *Resource Physiology of Conifers: Acquisition, Allocation, and Utilization*. Academic Press, New York, pp. 301–373.
- Park, A.D., 2001. Environmental influences on post-harvest natural regeneration in Mexican pine–oak forests. *For. Ecol. Manage.* 144, 213–228.
- Parker, W.C., Pallardy, S.G., Hinckley, T.M., Teskey, R.O., 1982. Seasonal changes in tissue water relations of three woody species of the *Quercus–Carya* forest type. *Ecology* 63 (5), 1259–1267.
- Pase, C.P., 1969. Survival of *Quercus turbinella* and *Quercus emoryi* in an Arizona chaparral community. *Southwest Nat.* 14, 149–156.
- Pugnaire, F.I., Haase, P., 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77 (5), 1420–1426.
- Putz, F.E., Canham, C.D., 1992. Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. *For. Ecol. Manage.* 49, 267–275.
- Quintana-Ascencio, P.F., Gonzalez-Espinosa, M., Ramirez-Marcial, N., 1992. Acorn removal, seedling survivorship, and seedling growth of *Quercus crispipilis* in successional forests of the highlands of Chiapas, Mexico. *Bulletin of the Torrey Botanical Club*, 119 (1), 6–18.
- Raffaele, E., Veblen, T.T., 1998. Facilitation by nurse shrubs of resprouting behavior in a post-fire shrubland in northern Patagonia Argentina. *J. Veg. Sci.* 9, 693–698.
- Raison, R.J., Khanna, P.K., Benson, M.L., Myers, B.J., McMurtrie, R.E., Lang, A.R.G., 1992. Dynamics of *Pinus radiata* foliage in relation to water and nitrogen stress. II. Needle loss and temporal changes in total foliage mass. *For. Ecol. Manage.* 52, 159–178.
- Reich, P.B., Walters, M.B., Ellsworth, D.S., 1992. Leaf lifespan in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecol. Mongr.* 62, 365–392.
- Rey Benayas, J.M., 1998. Growth and survival in *Quercus ilex* L. seedlings after irrigation and artificial shading on Mediterranean set-aside agricultural land. *Ann. Sci. For.* 55, 801–807.
- Richards, J.H., Caldwell, M.M., 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia (Berlin)* 73, 486–489.
- Ritchie, G.A., Hinckley, T.M., 1975. The pressure chamber as an instrument for ecological research. *Adv. Ecol. Res.* 9, 164–254.
- Royce, E.B., Barbour, M.G., 2001. Mediterranean climate effects. I. Conifer water use across a Sierra Nevada ecotone. *Am. J. Bot.* 88 (5), 911–918.
- Rzedowski, J., 1978. *Vegetation of Mexico*. Limusa, Mexico City, 432 pp.
- Sala, A., Tenhunen, J.D., 1994. Site-specific water relations and stomatal response of *Quercus ilex* in a Mediterranean watershed. *Tree Physiol.* 14, 601–617.
- Salas, S.H., Ramírez, G., Schibli, L., de Avila, A., Aguilar, R., 1994. Análisis de la vegetación y el uso de la tierra actual en el estado de Oaxaca. II. Regiones de Valles Centrales, Sierra

- Norte, y Papaloapan. La Sociedad para Estudios de los Recursos Bióticos de Oaxaca, A.C.
- Salleo, S., Nardini, A., Gullo, M.A.L., 1997. Is sclerophylly of Mediterranean evergreens an adaptation to drought? *New Phytol.* 135, 603–612.
- Sarmiento, F.O., 1997. Arrested succession in pastures hinders regeneration of Tropicandean forests and shreds mountain landscapes. *Conservation* 4 (1), 14–23.
- SAS Institute, Inc. 1995. Cary, NC.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5 (1), 18–32.
- Schoettle, A.W., Fahey, T.J., 1994. Foliage and fine root longevity of pines. *Ecol. Bull. (Copenhagen)* 43, 136–153.
- Shumway, D.L., Steiner, K.C., Kolb, T.E., 1993. Variation in seedling hydraulic architecture as a function of species and environment. *Tree Physiol.* 12, 41–54.
- Stone, C., Bacon, P.E., 1995. Leaf dynamics and insect herbivory in a *Eucalyptus camaldulensis* forest under moisture stress. *Aust. J. Ecol.* 20, 473–481.
- Thadani, R., Ashton, P.M.S., 1995. Regeneration of Banj oak (*Quercus leucotricophora* A. Camus) in the central Himalaya. *For. Ecol. Manage.* 78, 217–224.
- Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1, 511–523.
- Vance, N.C., Zaerr, J.B., 1991. Influence of drought stress and low irradiance on plant water relations and structural constituents in needles of *Pinus ponderosa* seedlings. *Tree Physiol.* 8, 175–184.
- Veenendaal, E.M., Swaine, M.D., Agyeman, V.K., Blay, D., Abebre, I.K., Mullins, C.E., 1995. Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *J. Ecol.* 83, 83–90.
- Waring, R.H., Franklin, J.F., 1979. Evergreen coniferous forests of the Pacific Northwest. *Science* 204, 1380–1386.
- Weltzin, J.F., McPherson, G.R., 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* 112, 156–164.
- Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy: the effects of fragmentation on extinction. *Am. Nat.* 125, 879–887.
- Zavala, M.A., Espelta, J.M., Retana, J., 2000. Constraints and trade-offs in Mediterranean plant communities: the case of Hom Oak–Aleppo Pine forests. *Bot. Rev.* 66 (1), 119–149.