

Sapling survival and growth of coniferous and broad-leaved trees in successional highland habitats in Mexico

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Abstract. We assessed survival and growth of transplanted saplings of understory broad-leaved trees (*Oreopanax xalapensis*, *Rapanea juergensenii*, *Rhamnus sharpii* and *Ternstroemia lineata*) and canopy conifers (*Abies guatemalensis*, *Pinus ayacahuite* and *P. pseudostrabus*) into Grassland (GR), Mid-Successional Oak Forest (MS), and Old-Growth Oak Forest (OF) stands in the central highlands of Chiapas, Mexico. A total of 727 plants were monitored over eight years. The results suggest habitat preferences of the studied species that should be considered for their conservation oriented management. Conifers had highest survival and growth in GR, while broad-leaved trees survived better under sparse canopy in MS, but grew tallest in full light. Saplings of all species in dense canopy sites in OF were smaller, and the survival of conifers was lower. An integrated response index (*IRI*) calculated for each species with survival and relative growth rates showed similar trends. Re-introduction of the endangered *A. guatemalensis* is possible in open habitats if fire, trampling and grazing are suppressed. Open habitats in current man-made landscapes in the highlands of Chiapas may limit the establishment of understory trees requiring partial shade. Inclusion of such species in restoration programs has not been usual so far; yet, local and global interest in native species for such programs is increasing. Information on the response of these kind of species in contrasting habitats may help to incorporate them in the management of high-diversity forests that may follow pine plantations.

Keywords: *Abies guatemalensis*; Deforestation; Forest restoration; Human disturbance; *Pinus*; Secondary succession; Species enrichment; Understory tree.

Abbreviations: EBH = Estación Biológica Huitepec; GR = Grassland; *IRI* = Integrated Response Index; MS = Mid-Successional Oak Forest; OF = Old-Growth Oak Forest; *PPF* = photosynthetic photon flux; *RGR* = relative growth rate.

Nomenclature: Breedlove (1986) and Farjon & Styles (1997).

Introduction

Understanding successional processes and the consequences of human-induced disturbance on forest dynamics is fundamental for wise management. Assessment of tree seedling establishment, and survival and growth of saplings in secondary habitats provide guidelines for forest management and restoration practices in disturbed landscapes (Glitzenstein et al. 1986; Brown & Lugo 1994). Differences in sapling survival and growth rates in response to natural or human-induced disturbance may be critical for the recruitment of canopy species, with long-term consequences on forest structure and dynamics (Foré et al. 1997). Most attention has been given to survival of natural or planted saplings in relatively (or assumed) undisturbed forests (e.g. Turner 1990; Ashton 1995), but few long-term studies exist on tree recruitment in human-disturbed habitats (Clark et al. 1999; Mesquita et al. 2001; Guariguata & Dupuy 1997).

In the highlands of Chiapas and Guatemala, plants and wildlife have been used for centuries by Maya people for firewood, food, and other purposes. However, current land-use systems have severely altered and reduced the original large expanses of forest (Ochoa-Gaona & González-Espinosa 2000), compromising the persistence of many late-successional species vulnerable to habitat fragmentation and loss. Selective logging and the replacement of forest cover by crop fields and pastures, either permanently or under slash-and-burn systems, have greatly reduced floristic richness and simplified forest structure (Ramírez-Marcial et al. 2001; Galindo-Jaimes et al. 2002). In the tropical mountains of S Mexico, species richness and dominance of understory trees and shrubs are higher under closed *Pinus-Quercus* or *Quercus*-dominated canopies than in more simplified *Pinus*-dominated stands. Most *Pinus* spp. may colonize open and relatively dry habitats, such as those created by human disturbance in temperate and tropical mountain regions (Richardson & Bond 1991). In old-growth forests, *Pinus*

spp. are pioneers and their juveniles occur in transient gaps, but some individuals may become emergent elements of the canopy in drier sites (Glitzenstein et al. 1986; González-Espinosa et al. 1991).

Over the last two decades the Mexican Government has devoted effort and resources to restore degraded forests, mostly using pines and species of exotic genera as *Casuarina* and *Eucalyptus*, and to a lesser extent the native *Cupressus lusitanica*. There is little interest in developing practices for management of forests with more complex structure and composition. Yet, conservation-oriented interest in native broad-leaved species is increasing, and information on their biology and silvics is urgently needed. Plantations and rehabilitated forests using native trees may provide sites for the establishment of other native trees, and would offer also benefits through wildlife management and ecological conservation (Parrotta 1995; Butterfield 1995).

In this study, we evaluate the survival and growth of transplanted saplings of four understory broad-leaved species and three canopy conifers into grasslands, open canopy forests previously harvested for firewood and oak timber, and closed canopy forests without evidence of disturbance. We hypothesized that conifers would survive better and grow taller than broad-leaved species in open sites, while the reverse would occur under closed canopies.

Material and Methods

Study area and successional communities

The study was conducted at the Estación Biológica Huitepec (EBH; Ramírez-Marcial et al. 1998), in central Chiapas, Mexico (16°44' N, 92°38' W, 2300-2680 m a.s.l.). The EBH (136 ha) is located on the summit and NE slope of a cinder cone surrounded by a plateau of Tertiary limestone. The regional climate is cold temperate with a mean temperature of 13-16 °C, and 1100-1300 mm of annual rainfall, occurring mostly between May and October (García 1987). The frequent presence of fog attenuates desiccation during the dry season. Nocturnal frosts may occur in open areas between December and March, but not in the forest understory. The soils are shallow (< 50 cm) sandy loams. Oak Forest (*Encinar*; Miranda & Hernández-Xolocotzi 1963) and Evergreen Cloud Forest (Breedlove 1981) cover most of the area above 2450 m. Secondary forests and isolated grasslands intermingle with old-growth stands at lower elevations. Disturbances were permanently eliminated within the preserve in 1988. Two replicate plots were located within an altitudinal belt (2350-2500 m) in the following successional stages:

1. Old-Growth Oak Forest (OF). It occupies the summits, ravines and steep slopes. *Quercus laurina*, *Q. crassifolia* and *Q. rugosa* dominate a closed canopy (20-25 m high), but a few large individuals of *Oreopanax xalapensis*, *Styrax argenteus* var. *ramirezii*, *Cleyera theaeoides*, *Persea americana* and *Clethra macrophylla* can be present. The understory tree layer (3-20 m high, but mostly < 10 m) includes 45-48 species. Epiphytes are very abundant and several large ferns (> 1 m tall) dominate the herbaceous layer. No signs of human disturbance are evident.

2. Mid-Successional Oak Forest (MS). It is the most extensive type of forest, has been subjected to light extraction of firewood, and was slightly logged 20-30 yr ago. The canopy is sparse and dominated by *Quercus* spp. and *Arbutus xalapensis*. The understory tree layer includes 20-25 species. Some timber and firewood for charcoal were harvested a decade before this study.

3. Grassland (GR). This type covers two areas of 1.5 and 5 ha cleared for agriculture, which were subsequently abandoned and grazed by sheep. *Baccharis vaccinioides*, *Monnina xalapensis*, *Viburnum elatum*, *Eupatorium* spp., *Buddleia cordata*, and *Alnus acuminata* ssp. *arguta* dominate a sparse woody layer (> 3 m). A discontinuous layer of bunch grasses (80-120 cm) includes *Muhlenbergia* spp., *Stipa* spp., *Trisetum irazuense* and *Festuca amplissima*.

Species

Three coniferous canopy species were chosen whose saplings were readily available at local nurseries, *Abies guatemalensis*, *Pinus ayacahuite* and *P. pseudostrobus* var. *apulcensis* (Farjon & Styles 1997). *A. guatemalensis* is an endangered and overexploited species whose distribution is limited to a few localities in southern Mexico and Guatemala (Walter & Gillett 1998); its natural regeneration is almost null (N. Ramírez-Marcial pers. obs.). *P. ayacahuite* and *P. pseudostrobus* are common elements in secondary stands throughout the region; both species have high economic value, and their recruitment may be abundant in open areas near reproductive adults. Four broad-leaved understory trees were also used: *Oreopanax xalapensis*, *Rapanea juergensenii*, *Rhamnus sharpii* and *Ternstroemia lineata* ssp. *chalicophila*. At the start of this study information on their reproductive biology or on how to produce their seedlings in a nursery was not available. We used naturally-recruited saplings of these broad-leaved trees, as they are abundant in nearby old-growth forest fragments. *Oreopanax*, *Rapanea*, *Rhamnus* and *Ternstroemia* are abundantly recruited under dense canopies, where they are frequently harvested for timber, firewood, and other traditional uses.

Transplant and study variables

In June-July 1989 we transplanted 727 saplings in the two plots of OF, MS and GR. Saplings (38-42 months old) of *Abies* (121 individuals, 15-29 plants per plot; mean initial stem height 10.6 cm ± 0.34 SE), *Pinus ayacahuite* (125 individuals, 18-29 plants per plot, 24.5 ± 0.55 SE), and *P. pseudostrobus* (152 individuals, 23-30 plants per plot, 24.7 ± 0.40 SE) were provided by a local nursery. Saplings (5-7 months old) of the broad-leaved trees were collected in November-December 1988 in old-growth stands at Rancho Merced-Bazom (ca. 22 km E of EBH; González-Espinosa et al. 1991). Plants per plot were 12-19 for *Oreopanax* (93 plants total, mean initial stem height 4.4 cm ± 0.14 SE), 15-17 for *Rapanea* (92 total, 5.0 cm ± 0.16 SE), 10-16 for *Rhamnus* (83 total, 8.7 cm ± 0.26 SE), and 8-13 for *Ternstroemia* (61 total, 8.1 cm ± 0.24 SE). All plants were kept outdoors under partial tree shade for 6-8 wk in plastic containers (1250 cm³ for conifers and 300 cm³ for broad-leaved trees), and were watered 3-4 times weekly before being transplanted. We discarded plants with very small or large sizes, or with obvious damage by insects or pathogens. No evidence of pre-transplant stress was observed in any species.

Coniferous saplings were transplanted every 5 m along 3-5 transects. Saplings of broad-leaved species were transplanted at the vertices of a square (1 m per side) between two transplanted conifers. Conifers were distributed over the plots to maximize species interspersions. Plants were mapped and marked with a plastic numbered tag. Survival and stem height were recorded two weeks after transplanting, and at 5, 8, 12, 16, 21, 28, 62, and 96 mo. Basal stem diameter was measured with calipers starting at 8 mo for conifers and 12 mo for broad-leaved species. Relative growth rates [$RGR = \ln(X_2/X_1)/t_2 - t_1$] of stem height and basal stem diameter were calculated after 62 months. For each species an integrated response index (*IRI*, De Steven 1991) was calculated at 62 months as $IRI = \text{survival proportion} \times RGR_{\text{height}} \times RGR_{\text{diameter}}$. A sunfleck ceptometer (Delta-T Devices, Ltd., Cambridge, UK) was used to measure photosynthetic photon flux (*PPF*) at 1 m above the ground (every 5 m along a 75-m random transect) in each habitat on January 29, 1995. Measurements were taken between 09.00 and 13.00 hr under clear skies.

Fig. 1. Mean (± 1 SE) sapling survival of studied tree species after transplantation into three successional habitats in July 1989. Error shown calculated with percent survival in two replicate plots. Lines with the same letter are not significantly different [Wilcoxon (Gehan) test, $p < 0.05$].

Analysis

We checked differences among heights of plants randomly allocated to habitats and replicates at the time of transplanting with one-way nested ANOVA (replicates within habitat). We compared (overall and pairwise) the shape of survival curves over 96 mo with the Wilcoxon (Gehan) generalized test. At the end of the study, sapling mortality resulted in unequal and small sample sizes in some replicate plots (1-5 ind.). Therefore, only mean height and basal stem diameter data collected up to 62 mo were analysed, and we pooled available data for each successional condition, and performed Kruskal-Wallis and Mann-Whitney pairwise tests to compare effects of successional habitats on stem height and basal stem diameter as well as on their relative growth rates. Analyses were carried out with SPSS, v.10.0 (Anon. 1999).

Results

Survival

After 96 mo all species had different survival in seral habitats which were widely different in their general light conditions. On a typical late winter day, *PPF* values (mean ± 1 SD) were highest in GR (620 ± 229.2 μmol.m⁻².sec⁻¹), intermediate in the highly variable MS (58 ± 103.9 μmol.m⁻².sec⁻¹), and lowest in the OF (10 ± 9.1 μmol.m⁻².sec⁻¹). Across habitats transplants generally had the highest survival for all species in MS (Fig. 1).

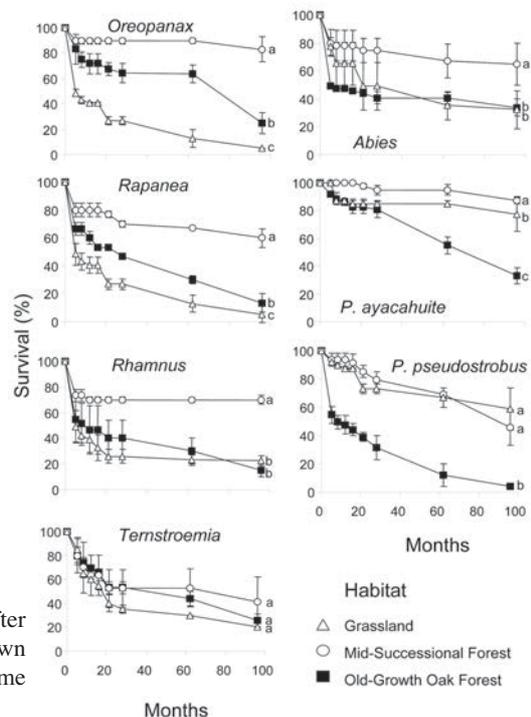


Table 1. Mean (\pm SE) of initial and final stem height and basal stem diameter, and Kruskal-Wallis tests on relative growth rates (*RGR*) of saplings of seven tree species after 62 mo of being transplanted into three successional habitats. Mean ranks with the same letter were not significantly different ($p < 0.05$, pairwise Mann-Whitney *U*-tests). OF = Old-Growth Oak Forest; MS = Mid-Successional Oak Forest; GR = Grassland. For basal stem diameter initial sample sizes and measurements correspond to 8 or 12 mo after transplantation for coniferous and broad-leaved species, respectively.

Species	Height (cm)					Basal stem diameter (cm)			
	Habitat	<i>N</i>	Initial Mean	62 mo after transplant <i>N</i> Mean	Mean rank	<i>N</i>	Initial Mean	62 mo after transplant Mean	Mean rank
<i>Oreopanax xalapensis</i>									
OF	27	4.5 \pm 0.25	16	45.5 \pm 8.33	12.81 ^a	19	0.35 \pm 0.04	0.61 \pm 0.07	11.31 ^a
MS	29	4.7 \pm 0.26	26	119.9 \pm 9.74	31.62 ^b	26	0.39 \pm 0.02	1.25 \pm 0.09	32.54 ^b
GR	37	3.9 \pm 0.20	5	53.0 \pm 18.58	20.20 ^a	15	0.39 \pm 0.04	0.87 \pm 0.23	20.20 ^{ab}
				$\chi^2 = 19.06, p < 0.0001$				$\chi^2 = 24.17, p < 0.0001$	
<i>Rapanea juergensenii</i>									
OF	30	4.7 \pm 0.22	9	21.1 \pm 2.04	14.89 ^a	16	0.23 \pm 0.02	0.36 \pm 0.03	8.39 ^a
MS	30	5.4 \pm 0.34	20	34.8 \pm 4.54	15.50 ^a	24	0.24 \pm 0.01	0.55 \pm 0.04	18.77 ^b
GR	32	5.0 \pm 0.23	4	71.3 \pm 8.76	29.25 ^b	7	0.29 \pm 0.03	0.91 \pm 0.09	27.50 ^c
				$\chi^2 = 7.34, p = 0.026$				$\chi^2 = 12.56, p = 0.002$	
<i>Rhamnus sharpii</i>									
OF	25	8.8 \pm 0.49	8	117.1 \pm 44.65	13.13 ^a	13	0.23 \pm 0.03	0.93 \pm 0.27	16.56 ^a
MS	27	8.9 \pm 0.51	19	121.5 \pm 12.28	18.37 ^a	19	0.30 \pm 0.02	0.89 \pm 0.07	16.76 ^a
GR	31	8.5 \pm 0.37	7	142.9 \pm 31.76	20.14 ^a	10	0.31 \pm 0.03	1.28 \pm 0.34	20.57 ^a
				$\chi^2 = 2.18, p = 0.34$				$\chi^2 = 0.84, p = 0.66$	
<i>Ternstroemia lineata</i>									
OF	23	7.8 \pm 0.31	10	23.7 \pm 3.24	7.55 ^a	15	0.23 \pm 0.02	0.37 \pm 0.04	7.85 ^a
MS	18	8.0 \pm 0.43	9	45.6 \pm 5.00	16.61 ^b	11	0.29 \pm 0.02	0.66 \pm 0.06	14.72 ^b
GR	20	8.6 \pm 0.53	6	68.8 \pm 26.01	16.67 ^b	11	0.31 \pm 0.03	1.13 \pm 0.33	19.00 ^b
				$\chi^2 = 9.16, p = 0.010$				$\chi^2 = 9.38, p = 0.009$	
<i>Abies guatemalensis</i>									
OF	44	10.8 \pm 0.51	17	50.7 \pm 5.90	15.94 ^a	21	0.32 \pm 0.02	0.58 \pm 0.05	14.12 ^a
MS	39	10.4 \pm 0.63	25	83.7 \pm 10.65	27.14 ^b	29	0.34 \pm 0.02	0.86 \pm 0.07	28.70 ^b
GR	38	10.7 \pm 0.67	14	172.6 \pm 11.45	46.18 ^c	26	0.51 \pm 0.03	2.34 \pm 0.23	45.61 ^c
				$\chi^2 = 26.71, p < 0.0001$				$\chi^2 = 28.64, p < 0.0001$	
<i>Pinus ayacahuite</i>									
OF	47	24.6 \pm 1.00	25	78.9 \pm 7.08	23.20 ^a	40	0.49 \pm 0.02	0.79 \pm 0.06	17.94 ^a
MS	40	25.0 \pm 0.88	38	111.6 \pm 8.78	39.63 ^b	40	0.50 \pm 0.02	1.17 \pm 0.08	41.30 ^b
GR	38	23.9 \pm 0.95	33	436.7 \pm 19.21	77.88 ^c	34	0.96 \pm 0.03	8.54 \pm 0.32	79.94 ^c
				$\chi^2 = 61.18, p < 0.0001$				$\chi^2 = 74.67, p < 0.0001$	
<i>Pinus pseudostrobus</i>									
OF	56	24.1 \pm 0.63	7	64.3 \pm 4.59	12.71 ^a	27	0.52 \pm 0.03	0.67 \pm 0.04	9.93 ^a
MS	48	24.1 \pm 0.69	33	119.4 \pm 10.08	25.67 ^b	45	0.50 \pm 0.02	1.32 \pm 0.14	25.47 ^b
GR	48	26.0 \pm 0.77	32	342.4 \pm 26.11	52.88 ^c	41	0.93 \pm 0.05	7.72 \pm 0.62	53.69 ^c
				$\chi^2 = 37.48, p < 0.0001$				$\chi^2 = 42.04, p < 0.0001$	

Mortality in GR was associated with open areas between shrubs (mostly *Baccharis vaccinioides*). We found in December 1992 that 68 out of 75 dead transplants in GR were located far from shade by shrubs or trees, while 22 out of 46 alive individuals were near to another woody species ($\chi^2 = 23.2$; $p < 0.001$; 1 df). The three coniferous species had lower survival in OF (*Abies* 32%; *P. ayacahuite* 33%; *P. pseudostrobus* 4%) than in MS (75, 88 and 46%, respectively). Survival of pines in GR was similar to that in MS (77 and 59%); the survival of *Abies* in OF was similar to that in GR (ca. 32%). Most conifers in GR were killed by pocket gophers (*Orthogeomys grandis*) during the first months after transplanting. Five large pines were harvested by people unrelated to the project before the last evaluation in August 1997. Mortality of *Rhamnus* and *Ternstroemia* was equally low in both OF and GR; *Oreopanax* and *Rapanea* had lower survival in open areas (Fig. 1).

Growth

After 62 mo mean height and basal stem diameter of saplings differed among habitats (Kruskal-Wallis test, all $p \leq 0.006$); similar trends were obtained with the *RGR* of these two variables (Kruskal-Wallis tests, all $p \leq 0.026$, Table 1). These trends continued to the end of the study (Figs. 2 and 3). Most species attained their greatest heights and basal stem diameters in GR (Figs. 2 and 3, Table 1), and had their shortest and thinner individuals in OF. Exceptions were *Rhamnus*, whose height and basal stem diameter did not differ significantly across habitats, and *Oreopanax*, which grew more in MS (Figs. 2 and 3). The range of variation in growth variables was larger among conifer species than among broad-leaved trees. Final mean height of conifers ranged between 0.75 m and 1.87 m in forested habitats, and 3.76 m and 7.43 m in GR (Fig. 2). Final mean basal stem diameter of the conifers

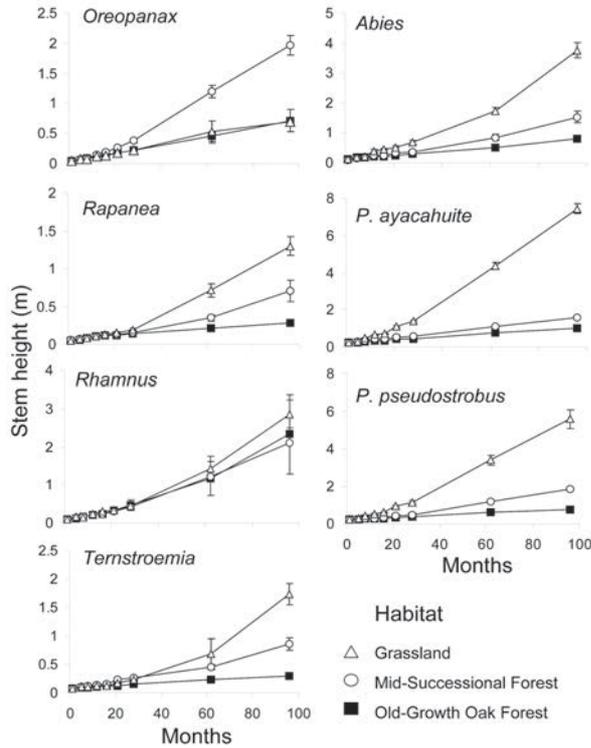


Fig. 2. Mean (± 1 SE) height of saplings of studied tree species after transplantation into three successional habitats in July 1989. Error shown calculated with total number of saplings in each successional stage.

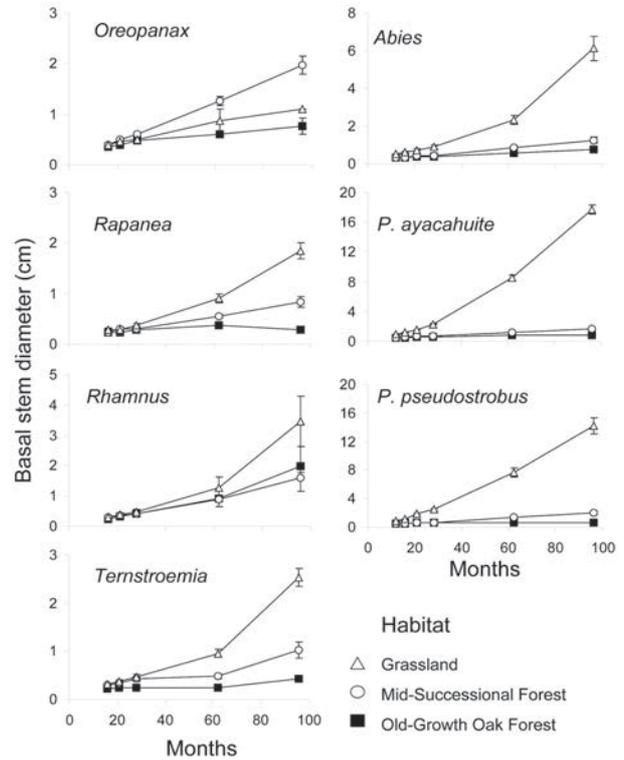


Fig. 3. Mean (± 1 SE) basal stem diameter of saplings of studied tree species after transplantation into three successional habitats in July 1989. Error shown calculated with total number of saplings in each successional stage.

ranged between 0.57 cm and 1.68 cm in forested habitats, and 6.1 cm and 17.7 cm in GR (Fig. 3). Differences between conifers in the open and forested habitats were evident from ca. 2 yr after being transplanted.

Integrated response index

According to the values of the integrated response index (*IRI*), 62 months after the transplantation in the field, a separation of the studied species in two major groups could be confirmed: canopy trees and understory trees (Fig. 4). All canopy tree species had their highest *IRI* values in GR, and their lowest in OF; *P. ayacahuite* outperformed the other two canopy tree species in GR. Individuals of broad-leaved species (except *Ternstroemia*) in MS outperformed their conspecifics in GR and OF; *Oreopanax* showed the most contrasting response among habitats (Fig. 4).

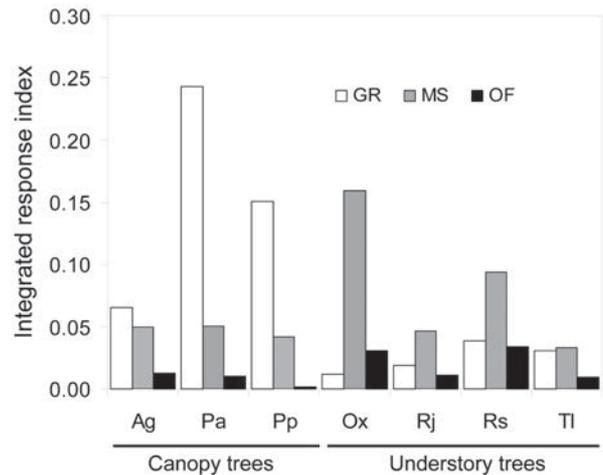


Fig. 4. Integrated response index ($IRI = \text{survival proportion} \times RGR_{\text{height}} \times RGR_{\text{diameter}}$) after 62 mo of seven tree species after transplantation into three successional habitats in July 1989. Ag = *Abies guatemalensis*; Pa = *Pinus ayacahuite*; Pp = *P. pseudostrobus*; Ox = *Oreopanax xalapensis*; Rj = *Rapanea juergensenii*; Rs = *Rhamnus sharpii*; Tl = *Ternstroemia lineata*.

Discussion

Habitat effects on survival and growth

Saplings of tree species in tropical mountain stands in southern Mexico differ in survival and growth patterns among successional habitats in human disturbed forests. Plant growth and survival in forests change in response to light availability related to disturbance events (Watling et al. 1997; Montgomery & Chazdon 2002). Differences in light environment further determine the levels of other physical variables, such as understory temperature, relative humidity, and water content in the soil. In this study, the old-growth forest habitat had a deeply shaded understory (ca. 2% of full sun at ground level), but *PPF* values in MS were an order of magnitude higher (10-25%), though highly variable. Nearby our study area (I. Romero-Nájera pers. comm.) more extreme and variable temperature and relative humidity were recorded in open habitats (mean weekly minimum temperature of 5 °C, mean weekly maximum temperature of 32 °C, mean weekly maximum daily temperature oscillation 24 °C, and maximum yearly oscillation of relative humidity of 94%) in comparison with the understory of *Pinus*-dominated secondary forests (6, 32, and 24 °C, and 78%, respectively), and *Quercus* old-growth forest, similar to ours (7, 23, and 12 °C, and 73%, respectively); early morning frosts (down to -3°) were only recorded in open habitats.

We used differently-aged plants for coniferous (ca. three years old) and understory tree species (ca. 6-months old). This could compromise comparisons among both species groups in rather short-term studies (e.g. less than two years after transplantation). Yet, the responses to different habitats that we found eight years later at the end of the study were very contrasting. *Abies* and *Pinus* had highest survival and growth in open areas, while broad-leaved understory trees survived better under more discontinuous canopy in mid-successional forest, but usually reached the highest stature in full light. On the other hand, closed canopies conditions in OF were most unfavourable for both survival and growth of all broad-leaved species. With the exception of *Oreopanax*, which showed a similarly poor growth in both open and closed habitats, our results with broad-leaved tree species can be interpreted under the hypothesis that a trade-off exists between low survival and high growth under high light conditions (Kitajima 1994; Walters & Reich 1996; Figs. 1-3).

Light gradient partitioning among species

Light gradient partitioning among coexisting tree species have been found for other tropical and temperate forests (Kobe 1999; Montgomery & Chazdon 2002). We use shade-tolerance differences of two *a priori* distinct groups (canopy vs. understory trees) to explore the mechanisms underlying their coexistence. Low light levels inside of forested habitats were detrimental for survival and growth of *Pinus* spp. and *Abies*, which seem to depend on the existence of natural forest gaps (e.g. Battles et al. 1995), or partial canopy clearing due to selective logging or fuelwood extraction. Individuals of the three coniferous species attained their highest values of the integrated response index (*IRI*) when transplanted into the open habitats (Fig. 4).

The broad-leaved tree species differed in their shade tolerance when responses were evaluated with the index integrating survival and growth. The more heterogeneous conditions in MS appear to be more favourable for broad-leaved species, except *Ternstroemia* (Fig. 4). *Oreopanax* outperformed the other broad-leaved species under the sparse canopy of MS; seedlings and saplings of *Oreopanax* may be common in secondary stands dominated by *Pinus* and *Quercus* (González-Espinosa et al. 1991). We observed at the end of the study a few (2-3) individuals of *Rhamnus sharpii* and *Oreopanax xalapensis* reaching reproductive stages only in open conditions. However, no information on pollinator activity, fruit set, and seed viability is available to suggest that open areas are more suitable habitats for *Rhamnus*.

Other factors varying among successional conditions could affect tree species survival. For example, changes in soil compaction and fertility in different microhabitats in abandoned logging roads resulted in differences in seedling density and species richness in lowland tropical forests (Guariguata & Dupuy 1997). Similarly, higher species richness and seedling densities were associated with sites abandoned without subsequent use in comparison with pastures before abandonment (Mesquita et al. 2001). Differences in understory colonization by native trees in plantations of exotic tree species were attributed to increasing visitation of dispersers in response to their preferences among the exotic species (Parrotta 1995). In our study sites, a high frequency of pocket gophers in the GR may also help to explain the lower survival of tree species there.

*Conservation of the endangered *Abies guatemalensis**

Our results suggest some habitat requirements for better conservation efforts of *Abies guatemalensis*. This is an endangered species (Walter & Gillett 1998) that

has been harvested by local people for timber and religious uses. *A. guatemalensis* is now a very rare species, as deforestation in favour of pastures and agricultural fields has increasingly replaced its natural habitat. The response of transplanted saplings observed in GR indicates that these open areas can be used for restoration practices, and that dense understory should be thinned in order to allow more incidental light at ground level for seedlings and saplings. The favourable survival and growth of saplings in GR suggests that other, more critical, factors limiting natural recruitment of *Abies* could be: (1) low density of reproductive adults and their clumped distribution; (2) low seed viability and germination (N. Ramírez-Marcial pers. obs.); (3) grazing by rabbits and pocket gophers; (4) grazing and trampling by free-ranging cattle; (5) fire incidence for agricultural purposes.

Management applications

Understanding the differences in growth and survival of tree species on successional gradients provides guidelines for management and conservation. In restoration practices aimed to species enrichment in tropical mountain stands, the establishment of broad-leaved trees may require the pre-existence or maintenance of a not too dense cover provided by shrubs (Ramírez-Marcial et al. 1996) or pines (Camacho-Cruz et al. 2000). In contrast, the use of pines for timber requires planting them in open areas (or in gaps at least 10-15 m diameter). The current widespread use of pines for commercial plantations in open habitats is supported by our results. However, species enrichment treatments involving native understory broad-leaved trees should be prescribed only after the conifer plantation has been established for 5-10 years.

Current landscapes in the study area may be limiting for understory trees. Increasing forest fragmentation and the dependence of this large species group on closed canopies may threaten their long-term persistence (about 350 understory tree species may occur in the central highlands of Chiapas; M. González-Espinosa pers. comm.). Seed survival and dispersal are critical stages for many understory trees in the region (Quintana-Ascencio et al. 1992), but forest stands subjected to traditional timber and firewood harvesting offer conditions allowing their natural regeneration (Camacho-Cruz et al. 2000). The recognition of different habitat requirements for the two distinct functional groups of species (conifers and broad-leaved trees), as well as their individual responses along the successional gradient, may contribute towards a more conservation-oriented silviculture and forest restoration in landscapes where traditional practices prevail.

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