AMERICAN JOURNAL OF Botany

SEEDLING FUNCTIONAL TYPES IN A LOWLAND RAIN FOREST IN MEXICO[1]

GUILLERMO IBARRA-MANRÍQUEZ,[2] MIGUEL MARTÍNEZ RAMOS, AND KEN OYAMA

Departamento de Ecología de los Recursos Naturales, Instituto de Ecología, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro 8701, Ex-Hacienda de San José de la Huerta, 58190, Morelia, Michoacán, México

Seedling morphology of 210 species (173 trees and 37 lianas) was studied from a community perspective to identify major patterns of seedling functional types in a Mexican rain forest. Five types of seedlings were distinguished: cryptocotylar with reserve storage or absorption cotyledons (epigeal [CER] and hypogeal [CHR]), phanerocotylar epigeal, either with photosynthetic cotyledons (PEF) or with reserve storage or absorption cotyledons (PER), and phanerocotylar hypogeal with reserve cotyledons (PHR). The most common seedling type was PEF (49.5%), followed by CHR (31.4%), PER (9.5%), PHR (7.2%), and CER (2.4%). Excepting the CER type, seedling type frequencies did not differ between trees and lianas. The PEF seedlings had the lightest seeds, whereas CHR seedlings had the heaviest ones. Pioneer trees showed lighter seeds than persistent trees or lianas in species with PEF but not in species with PER. Pioneer trees (38 species) showed three seedling types and the most common was PEF (82%). Persistent trees (135 species) showed the five seedling types but PEF (43%) and CHR (37%) were the most frequent. Seedling type frequencies differed among dispersal syndrome groups. The animal dispersal syndrome was significantly more frequent in species with CHR. Our results show an evolutionary convergence of seedling types at the community level worldwide and the existence of a phylogenetic inertia in the evolution of initial seedling morphology. A comparison among eight tropical communities indicated on average that PEF is the most frequent type and CER the least common, although the relative frequency of each seedling type differs among communities, particularly between Neotropical and Paleotropical sites.

Key words: angiosperm phylogeny; lianas; Mexico; seed dispersal; seedlings; seed size; trees; tropical rain forest.

Seedling emergence and establishment are critical early plant life cycle stages (e.g., Harper, 1977; Angevine and Chabot, 1979; Silvertown et al., 1993). Attributes of newborn seedlings such as size, function, position of cotyledons, and amount of maternal seed reserves may be crucial to capture resources, to cope with mortality agents, and to a plant's Darwinian fitness (e.g., Fenner, 1985). This suite of attributes constitutes the so-called initial seedling morphology or seedling type. Recently, an increasing interest has been directed to understand the evolutionary, functional, and ecological significance of these plant life history traits (e.g., de Vogel, 1980; Duke and Polhill, 1981; Hladik and Miquel, 1990; Kitajima, 1992, 1996; Leishman, Westoby, and Jurado, 1995; Garwood, 1996).

Different taxa tend to exhibit similar seedling types, suggesting the existence of a high degree of evolutionary convergence among distantly related taxa (e.g., Duke, 1965, 1969; Ng, 1978; del Amo, 1979; de Vogel, 1980; Barrera, 1985). In the literature on seedling morphology, different classifications have been provided. Most authors had proposed species classification using 2–5 types of seedlings (Duke, 1965, 1969; Ng, 1978; Garwood, 1983, 1996; Miquel, 1987; Hladik and Miquel, 1990). Recently, Garwood (1996) reviewed these classifications and established five seedling categories, which encompass most seedling morphological species variation, depending on the cotyledon's function and position. Although all

classifications are not 100% precise in defining a species seedling type, they have proved to be very useful in understanding the functional and ecological significance of initial seedling morphological traits (Garwood, 1996).

In tropical forests, the adaptive value of different seedling types has been explored analyzing seedling performance under environmental conditions that characterize open and closed-canopy (mature) forest patches. Seedlings of different types have different light requirements (de Vogel, 1980; Fenner, 1985). Seedlings that establish under shaded conditions often possess large amounts of seed reserves, which increase the probability of survival under light-limited conditions (e.g., Howe and Richter, 1982; Fenner, 1985; Foster, 1986; but see Metcalfe and Grubb, 1995). In contrast, seedlings of secondary forest species, which do not survive under the shade, have small seed reserves and photosynthetic cotyledons that enable them to grow fast in light-rich environments (Ng, 1978; Foster and Janson, 1985; Foster, 1986; Garwood, 1996; Kitajima, 1996). Some secondary herb species, like those in the Heliconiaceae and Zingiberaceae, have an endosperm or perisperm with high-quality reserves (Garwood, 1996).

The initial morphology of seedlings is associated with seed size and dispersal capacity (Augspurger, 1984; Martínez-Ramos and Soto-Castro, 1993; Garwood, 1996). For example, establishment of seedlings depends on interactions between forest environmental heterogeneity, seed dispersal, seed bank dynamics, and functional traits of seedlings (e.g., Alvarez-Buylla and Martínez-Ramos, 1990). At Los Tuxtlas, seedlings of tree species differing in initial morphology exhibited differential growth between gaps and mature forest (Popma and Bongers, 1988). Although all species showed increasing growth with light, species with epigeal seedlings and small, widely dispersed seeds had higher relative growth rates and

grew faster in biomass than hypogeal seedlings of large-seeded but poorly dispersed species.

Two routes may be taken to approach the analysis of the ecological significance of initial morphology of seedlings. One is the study of functional (e.g., morphological, physiological, and demographic) behavior of seedling types in different environments (e.g., Augspurger, 1984; Foster, 1986; Popma and Bongers, 1988; Ellison et al., 1993; Metcalfe and Grubb, 1995; Grubb and Metcalfe, 1996; Kitajima, 1996). The other is the use of a comparative approach, where general patterns of seedling establishment and seedling types are explored within and between communities (e.g., Hladik and Miquel, 1990; Martínez-Ramos and Soto-Castro, 1993; Garwood, 1996). Studies of the latter type have been done, for example, in a Malaysian evergreen forest (Ng, 1978), a semideciduous forest on Barro Colorado, Panama (Garwood, 1983), and an evergreen forest in Gabon, Africa (Miquel, 1987; Hladik and Miquel, 1990).

In this paper we approach the comparative study of seedling types using a set of 210 woody plant species from Los Tuxtlas rain forest, Mexico. We explore seedling type frequencies in relation to ecological attributes because different seedling types may be a sign of physiological adaptations for establishment in plants that differ in habit, vectors of dispersion, or life history. We also expect that phylogenetic relatedness among species may restrict such ecological variability. We addressed the following questions: (1) Does the frequency of seedling types vary among species differing in seed size, life form, dispersal syndrome, and successional position? (2) Is the frequency of seedling types associated with species taxonomic affinity? (3) Is the seedling type spectrum at Los Tuxtlas similar to that in other tropical forests?

MATERIALS AND METHODS

Study site—This study was conducted at La Estación de Biología Tropical Los Tuxtlas located in southeastern Mexico in the state of Veracruz. This 640-ha reserve belongs to the National University of Mexico (UNAM). The mean annual precipitation is 4560 mm, and the mean annual temperature is 23.7°C. The predominant vegetation is classified as lowland tropical high evergreen rain forest (Bongers et al., 1988; Ibarra-Manríquez et al., 1997). For a detailed description of Los Tuxtlas see González-Soriano, Dirzo, and Vogt (1997).

Classification of seedling types—Seeds of 173 tree and 37 liana species were gathered in different months during several years (1982–1991). This sample size is comparable with those reported in other communities (Garwood, 1996). Although these species did not represent the entire flora, they are a representative sample of the woody community. Our study at Los Tuxtlas included the most common trees and lianas and represent ~50% of the 412 woody species described in the area, which consists of 298 trees and treelets, 23 shrubs, and 91 lianas (Ibarra-Manríquez and Sinaca-Colín, 1995, 1996a, b). Seeds were cleaned, measured, and germinated in greenhouses (metallic frames covered with transparent nylon mesh with 4-mm² apertures) in sun and shade conditions at the Estación de Biología Tropical Los Tuxtlas. Seedlings were classified (see below), harvested, and dried for herbarium collection. A complete collection of plant specimens was deposited in the Herbario Nacional (MEXU) of the Instituto de Biología, UNAM and in the local herbarium at Los Tuxtlas station. Voucher numbers are available as supplementary material (http://ajbsupp.botany.org/v88/ibarra-manriquez.html and http://ajbsupp.botany.org/v88/ibarra-manriquez.xls). All seedling specimens have their respective voucher of mature plants (including seed collection) deposited at these herbaria (see Ibarra-Manríquez and Sinaca-Colín, 1995, 1996a, b).

Seedlings were classified according to the position (length of hypocotyl), exposition (cotyledons covered or uncovered by the seed coat), and function (cotyledons with photosynthetic or storage capacity), following the classification proposed by Garwood (1996). The terms epigeal and hypogeal refer to the position of cotyledons above vs. at or under ground level, respectively. The terms phanerocotylar and cryptocotylar refer to exposed and hidden cotyledons, respectively. Functionally, cotyledons may be leaf-like green (primarily photosynthetic) or fleshy food-storing (or endosperm absorbing) organs. Although eight different seedling types are possible combining these three criteria, only five seedling types are recognized: (1) PEF, phanerocotylar epigeal with foliaceous cotyledons; (2) PER, phanerocotylar epigeal with reserve storage or absorption cotyledons; (3) PHR, phanerocotylar hypogeal with reserve storage or absorption cotyledons; (4) CHR, cryptocotylar hypogeal with reserve storage or absorption cotyledons; and (5) CER, cryptocotylar epigeal with reserve storage or absorption cotyledons (Fig. 1). Both cryptocotylar hypogeal with photosynthetic cotyledons and cryptocotylar epigeal with photosynthetic cotyledons are seedling types biologically not possible, while phanerocotylar-hypogeal with photosynthetic cotyledons has been not recorded yet.

Seed size measurements and dispersal syndrome—We obtained ~30 seeds per species in order to assess species average seed dry mass. Seeds were obtained from mature fruits, cleaned, dried at 60°C, and weighed. In this study seeds are defined in a wide sense (i.e., diaspores), and they can include strictly seeds or also seeds together with some fruit structures, for example, the endocarp in the case of the genus *Calatola* (Icacinaceae). The dispersal syndrome of each study species was deduced from traits of the diaspores (fruits or seeds) and field observations. Fruits dispersed by birds and mammals included fleshy fruits or arillate seeds. The wind-dispersed species are those with fruits or seeds with laminar expansion like wings or trichomes. Explosive species possessed generally capsular fruits that eject their seeds at varied distances from the maternal plant. Species without any apparent characteristic described above were classified as dispersed by gravity. The association between seedling type and dispersal mode was assessed contrasting species with fleshy fruits or arillate seeds (basically bird and mammals dispersal) vs. nonanimal dispersal modes (wind, explosive, and gravity). This simple comparison was done because sample size was very small for the nonanimal dispersal mode.

Successional status of plant species—Recognizing that there is no universally accepted categorization for tree regenerative guilds in the tropics (Swaine and Whitmore, 1988), species were classified in two groups (pioneer and persistent or nonpioneer) based on their autoecology and the position they occupied in the natural regeneration of the forest. We followed the terminology used by Martínez-Ramos, Alvarez-Buylla, and Sarukhán (1989) from their demographic analyses in the same forest of Los Tuxtlas. Pioneer species mature and reproduce only under conditions of open light, as in large tree gaps, disturbed areas, or near cultivated lands. These plants may persist in the forest under more diffuse light such as older light gaps or the periphery of recent light gaps. Persistent species (nonpioneer) establish, and in some cases can mature and reproduce, under conditions of shade after the canopy has closed.

Statistical analyses—We used analysis of deviance (ANDEVA) to test single and interactive effects of life form (lianas, canopy, and subcanopy trees), dispersal mode (animal vs. others), and successional status (pioneer vs. persistent) on frequency of seedling types. In all analyses, we used Poisson error and log-link function as suggested for count variables, and when needed, overdispersion was corrected by appropriate scaling (Crawley, 1993). To test differences in seed mass among seedling types and life forms, we used one-way ANOVA transforming seed dry mass data into logarithms. Comparison of seedling type frequencies among different tropical communities was done using a log-linear model following GLIM procedures (Crawley, 1993).

To assess the influence of species phylogenetic relations on seedling type frequencies we performed two different analyses. At the family level, we obtained the relative frequency of families with species sharing the same seedling type as a function of the number of species per family. We grouped separately families with 2, 3, 4, 5–7, and 8–16 species. The last two broader categories were defined due to the small number of speciose families. For each group we obtained the proportion of families species of which have the
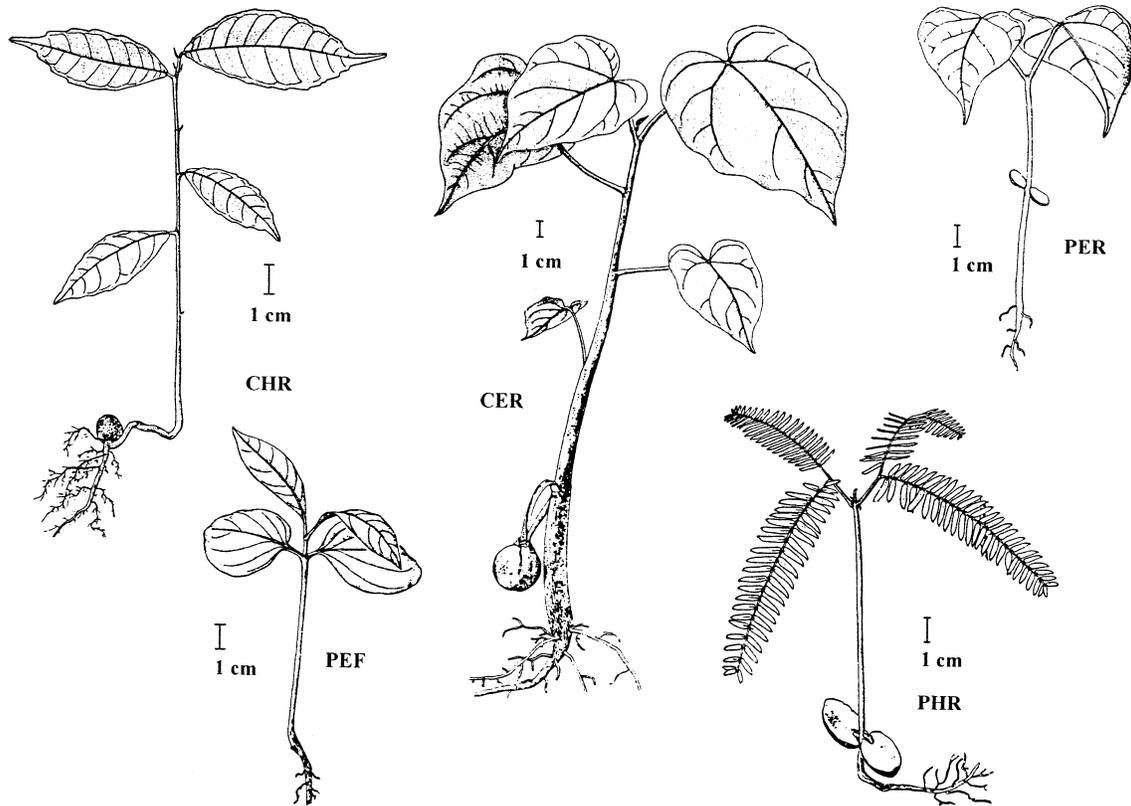
Fig. 1. The five seedling types (species with their family between parentheses): (1) CER, cryptocotylar epigeal with reserve storage or absorption cotyledons (*Omphalea oleifera*, Euphorbiaceae); (2) CHR, cryptocotylar hypogeal with reserve storage or absorption cotyledons (*Pseudolmedia oxyphyllaria*, Moraceae); (3) PEF, phanerocotylar epigeal with foliaceous cotyledons (*Psychotria faxlucens*, Rubiaceae); (4) PER, phanerocotylar epigeal with reserve storage or absorption cotyledons (*Erythrina folkersii*, Fabaceae); (5) PHR, phanerocotylar hypogeal with reserve storage or absorption cotyledons (*Cojoba arborea*, Mimosaceae). The original drawings were taken from del Amo (1979), all at scale 1 cm.

same seedling type. These proportions were contrasted with those generated by a null model, constructed by randomly sorting seedling types among families keeping the number of species per family constant. We ran this model 100 times and obtained the mean proportion of each group (± confidence interval). At clades higher than family level, we performed a correspondence analysis (Orden 2.0; Ezcurra, 1992). A matrix was constructed using seedling types as columns and families as rows; the number of species per family recorded by seedling type was used as cell frequency. For this analysis, only families with more than three species were used. We allocated families to high-order clades based on the angiosperm phylogenetic tree provided by Soltis, Soltis, and Chase (1999). Those few families that were not present in this tree were assigned to clades based on taxonomic and phylogenetic criteria given in Bhattacharyya and Johri (1998) and Judd et al. (1999). Finally, seedling type spectrum was obtained categorizing species in the following high-order clades: Eumagnoliids, Eurosid I, Eurosid II, Euasterid I, and Euasterid II. The resulting seedling type spectrum was mapped in the angiosperm phylogenetic tree provided by Soltis, Soltis, and Chase (1999). Statistical deviation of the seedling type spectrum of each clade, with respect to the one obtained pooling all species, was tested using chi-square analysis.

RESULTS

In total, seedlings of 173 tree and 37 liana species were successfully raised and classified. Species information on life form, seedling type, successional status, seed size, and mode of dispersal are available as supplementary material (http://ajbsupp.botany.org/v88/ibarra-manriquez.html and http://ajbsupp.botany.org/v88/ibarra-manriquez.xls)

Seedling types and life forms—Tree and liana groups did not differ in frequency of seedling types as the interaction seedling type × life form was not significant ($\chi^2 = 6.9$, df = 3, $P > 0.05$; the degree of freedom is three because we did not considered the CER type as it was not recorded in the liana group). The most common seedling type was PEF for both groups, followed by the CHR type. The CER seedling type was present in only five tree species (*Faramea occidentalis*, Rubiaceae; *Malmea depressa*, Annonaceae; *Omphalea oleifera*, Euphorbiaceae; *Trichilia martiana*, Meliaceae; and *Pimenta dioica*, Myrtaceae). We did not find significant differences in frequency of seedling types between canopy and subcanopy trees ($\chi^2 = 3.96$, df = 4, $P > 0.25$).

Seedling types and seed size—Average species seed mass varied from 0.001 to 22.5 g dry mass, although ~50% of species have seeds with masses between 0.13 and 1.03 g. Seed mass varied significantly among seedling types ($F_{4,180} = 30.3$, $P < 0.001$). The PEF seedlings had significantly lighter seeds, while CHR seedlings had heavier ones. The PHR, CHR, and CER seedlings did not differ in seed mass from each other (Fig. 2a). Comparing this characteristic among pioneer trees, persistent trees, and lianas, we found significantly lighter seeds in pioneer than persistent trees or lianas in species with PEF seedlings ($F_{2,86} = 11.0$, $P < 0.001$; Fig. 2b) but not among species showing PER seedlings ($F_{2,12} = 1.1$, $P > 0.25$; Fig.

(a)

(b) **(c)**
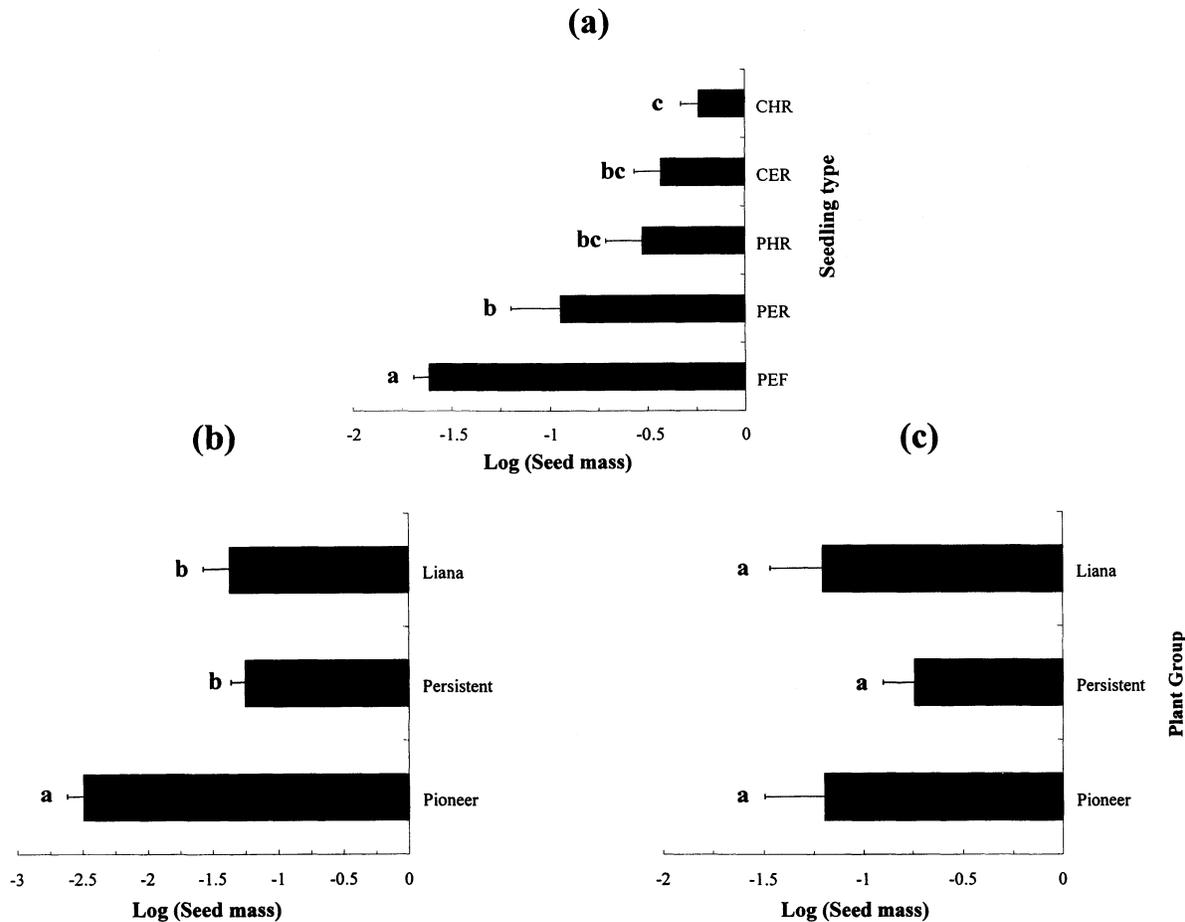
Fig. 2. Seed dry mass variation among species at Los Tuxtlas rain forest, Mexico (seed mass measured in grams). Variation partitioned (a) among seedling types, (b) among plant groups sharing PEF seedling type, and (c) among plant groups sharing the PER seedling type. Categories with the same letter were not significantly different at $P > 0.05$.

2c). The latter result, however, may be attributable to the small sample size analyzed.

Seedling types and mode of dispersal—The ANDEVA analysis showed that seedling type spectra differ between species with different dispersal syndrome, as indicated by the significant interaction between seedling type and dispersal mode ($\chi^2 = 25.4$, df $= 4$, $P < 0.001$). Overall, species with CHR seedlings showed a predominantly animal dispersal syndrome (Fig. 3a). Among tree species, animal dispersal mode was significantly associated with the CHR seedling type while the same situation occurred between nonanimal dispersal mode and the PEF seedling type (Fig. 3b). Among lianas, CHR seedlings were overrepresented. This pattern was not random as indicated by the significant dispersal mode $\times$ seedling type interaction ($\chi^2 = 12.2$, df $= 3$, $P < 0.001$).

Seedling types and successional status—Considering tree species, 38 were classified as pioneer species and 135 as persistent species. Among the species found in the former group we recorded all seedling types, but among pioneer species we did not find the PHR and CER seedling types. Excluding these two last types, PEF seedlings were significantly overrepresented among pioneer species and CHR seedlings among persistent species (Fig. 4a), as indicated by the significant seed-

ling type $\times$ successional status interaction in the ANDEVA analysis ($\chi^2 = 42.3$, df $= 2$, $P < 0.001$). Pioneer tree species did not show significant differences in frequency of seedling types (PEF and PER) between dispersal syndrome groups ($\chi^2 = 0.88$, df $= 1$, $P > 0.25$; Fig. 4b). Among persistent trees (Fig. 4c), species with the animal-dispersal mode showed significantly higher frequency of the CHR seedling type and significantly lower frequency of the PEF seedling type than non-animal dispersed species ($\chi^2 = 19.9$, df $= 4$, $P < 0.005$).

Seedling type spectra and taxonomic relations—The PEF seedling type was significantly most frequent, CHR was intermediate, and CER was significantly less common ($\chi^2 = 133.9$, df $= 4$, $P < 0.0001$; Table 1). The 210 study species belong to 65 families; the most common families were Bignoniaceae (16 species), Fabaceae (13 species), Rubiaceae (13 species), Mimosaceae (10 species), and Arecaceae (nine species). Twenty-four families had only one species, and 47 families (72.3 %) had less than three species. The most speciose genera were *Psychotria* (seven species, Rubiaceae), *Chamaedorea* (six species, Arecaceae), *Inga* (five species, Mimosaceae), and *Eugenia* (four species, Myrtaceae). A large proportion of diversity of woody plants at Los Tuxtlas forest is contained in many genera (159) with less than three species (see supplementary material).

(a)

(b)   **(c)**
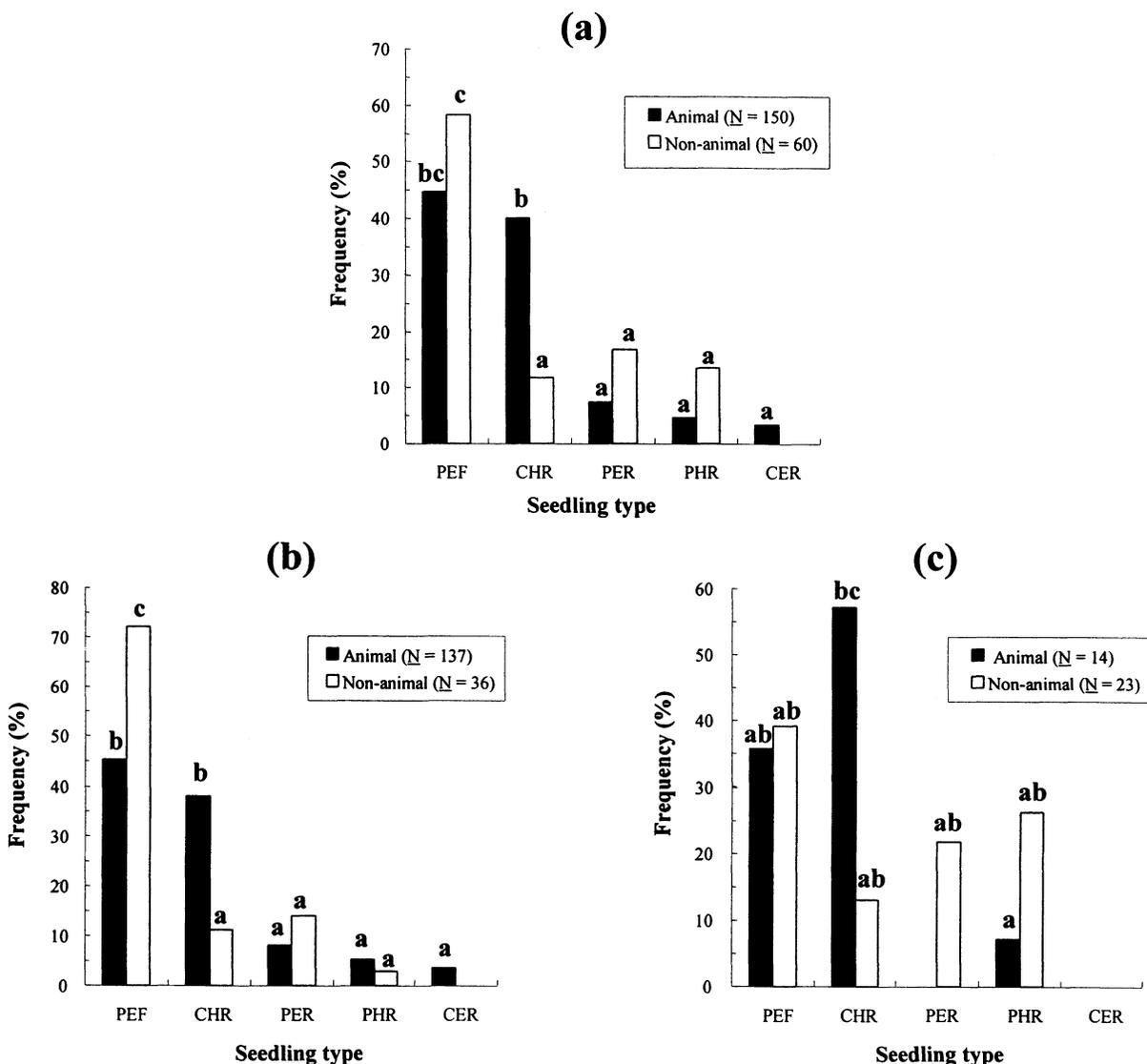
Fig. 3.   Association between seedling type and dispersal mode at Los Tuxtlas rain forest, Mexico. Dispersal mode variation among seedling type categories is shown for: (a) the whole study community, (b) tree species, and (c) liana species. Categories with the same letter were not significantly different at $P >$ 0.05.

The two most common families have different representation in life forms and seedling types. Bignoniaceae was a very diverse family with 13 genera, including 14 liana and 2 tree species; it had three types of seedlings (eight species with PEF, six species with PHR, and two with PER). In the Fabaceae, represented by 11 genera with 13 species (12 trees and 1 liana), we found all seedling types except CER. In contrast, at least 18 families had few genera and had only one predominant seedling type. For example, in Lauraceae (four genera, seven species) and Arecaceae (four genera, nine species), all species have CHR seedlings (see supplementary material).

Within genera, there were a limited number of seedling types. For example, all seven *Psychotria* (Rubiaceae) species showed PEF seedlings. Within *Acacia* (three species) and *Inga* (four species) all the species of these Mimosaceae genera share the same seedling type (PER and CHR, respectively). Twenty-nine genera have two or more species; in 25 genera, species shared the same seedling type (86.2%). In only four genera

(*Lonchocarpus, Pouteria, Senna,* and *Trichilia*), we find more than one seedling type.

Taxonomically, families represented by only two species had higher probability to have species with the same seedling type than speciose families, i.e., those represented by more than four species. The null model also produced this pattern, but the observed probabilities were significantly higher than that expected by random (Fig. 5). Even the families with more species (e.g., Arecaceae, Lauraceae, and Rubiaceae; see supplementary material) have notoriously higher probability to have species with same seedling type than that expected by random.

Correspondence analysis showed that taxon affinities at high-order clades partially clear up the differences in seedling type frequencies among families; the first two axes explained 76% of total variance (Fig. 6). Families in the Eumagnoliid clade did not have PHR and PER seedling types, families in the Rosid clade (Eurosid I and Eurosid II) were underrepre-
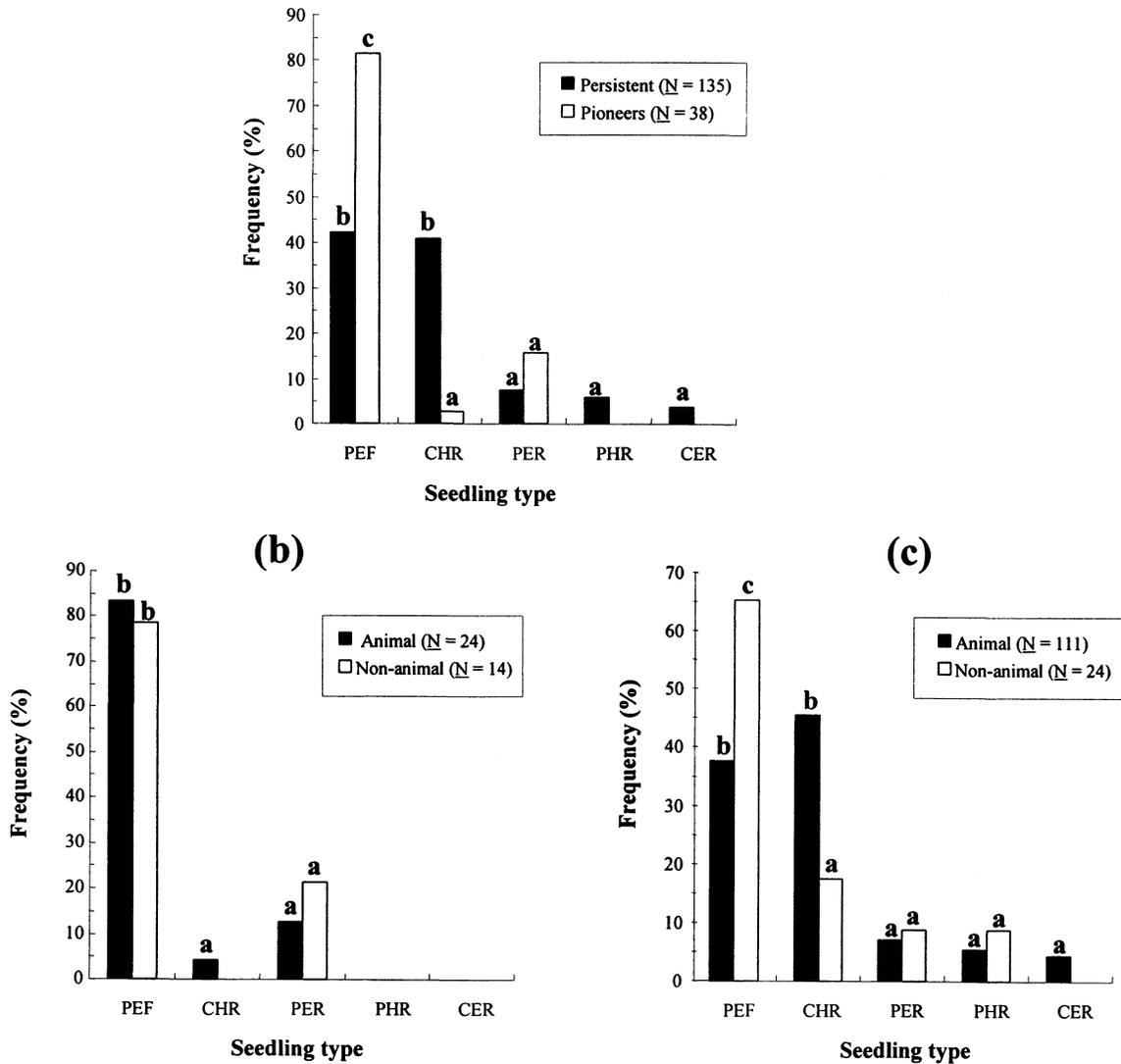
Fig. 4. Seedling type spectrum variation among successional and dispersal mode tree groups at Los Tuxtlas rain forest, Mexico. Variation of seedling type frequencies is shown between (a) pioneer and persistent tree species, (b) dispersal modes in pioneer tree species, and (c) dispersal modes in persistent tree species. Categories with the same letter were not significantly different at $P > 0.05$.

TABLE 1. Percentage of species with different seedling types at nine tropical localities (modified from Garwood, 1996). Seedling types: PEF (phanerocotylar epigeal with foliaceous cotyledons), PER (phanerocotylar epigeal with reserve storage or absorption cotyledons), CHR (cryptocotylar hypogeal with reserve storage or absorption cotyledons), PHR (phanerocotylar hypogeal with reserve storage or absorption cotyledons), and CER (cryptocotylar epigeal with reserve storage or absorption cotyledons). The PR column gives percentage of species with cotyledons functioning as reserve organs, lumping species with PER, CHR, PHR, and CER seedling types. The last column indicates species sample size for each locality. The values of CHR and PHR for Guadeloupe site were obtained from Fig. 3.2 in Garwood (1996). After χ^2 tests, significant deviation of each locality from the average seedling type spectrum (bottom) is indicated by * ($P < 0.005$). For each locality, significant deviation frequencies are indicated in boldface type.

Site	PEF	PER	CHR	PHR	CER	PR	N
Mexico*	49.5	**9.5**	**31.4**	7.2	2.4	50.5	210
Guadeloupe[ns]	51.0	15.7	22.0	9.3	2.0	49.0	102
Panama[ns]	42.9	16.1	28.8	8.8	3.4	57.1	205
Puerto Rico[ns]	48.1	18.1	23.8	8.8	1.3	52.0	160
Venezuela*	**56.2**	19.6	**14.4**	7.2	2.6	43.8	194
Indonesia*	32.7	18.7	28.7	12.0	**8.0**	67.4	150
Malaysia*	34.8	29.0	18.6	10.0	**7.6**	65.2	210
Gabon[ns]	39.0	24.8	21.9	9.0	5.2	60.9	210
Nigeria*	34.5	**43.4**	**11.5**	7.1	3.5	65.5	113
Means ± SE	43.2 ± 2.8	21.7 ± 3.3	22.3 ± 2.2	8.8 ± 0.5	4.0 ± 0.8	56.8 ± 2.8	
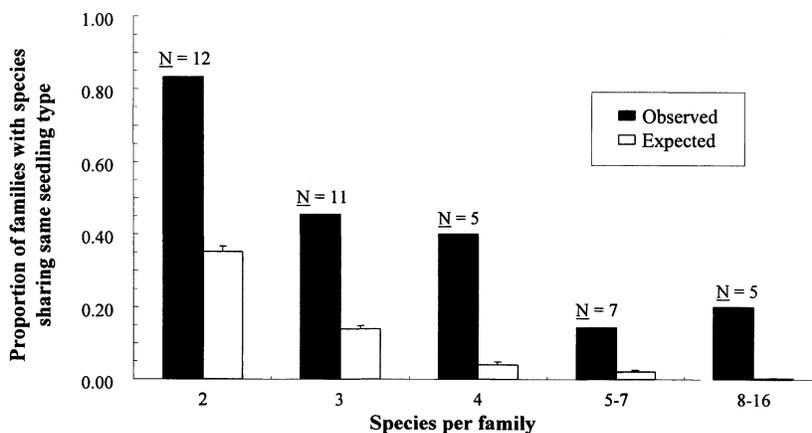
Fig. 5.   Constancy of same seedling type within families differing in species richness at Los Tuxtlas rain forest, Mexico. Black bars indicate observed frequencies and open bars the expected under a null random model. Vertical bars indicate 2 SE. See text for further details.

sented in CHR and PHR seedling types, while families in the Asterid clade (Euasterid I and Euasterid II) had predominately the PEF seedling type. However, some families belonging to different clades had similar seedling type frequencies; for example, Asteraceae (Euasterid II), Boraginaceae (Euasterids I), Flacourtiaceae (Eurosid I), and Piperaceae (Eumagnoliids) showed PEF seedlings (Fig. 6).

Mapping seedling type spectra of high-order clades into the angiosperm phylogenetic tree reinforced the results (Fig. 7). With respect to the seedling type spectra of all the sampled species, Eumagnoliids had a significantly higher frequency of CHR seedling type, and none of the species with PER and PHR seedling types were represented in this clade. Eurosid clades showed the same seedling type spectrum as that of the whole-species sample. Finally, Asterid clades showed significantly higher frequency of species with the PEF seedling type, particularly the Euasterid II clade, which did not have PER, PHR, and CER seedling types (Fig. 7).

Seedling type spectrum in Neotropical and Paleotropical rain forests—Species with PEF and CHR seedlings were predominantly abundant in the seedling type spectrum at Los Tuxtlas, while CER and PER seedlings had the lowest values (Table 1). An ordination analysis by principal components, based on the locality × seedling type matrix provided in Table 1, showed that along principal component 1, which explained 87.2% of the variance in seedling type spectra among sites, the Neotropical localities tended to have higher frequencies of PEF and CHR seedling types, while the Paleotropical localities displayed higher frequency of PHR, CER, and PER seedling types (Fig. 8). Indeed, considering the first principal component, there was a significant difference in average locality scores between Neotropical and Paleotropical sites (Mann-Whitney $U = 20.0$, $P = 0.008$). This difference was mostly due to the overrepresentation of the PEF seedling type in the Neotropical sites (Table 1). On average, the proportion of species with photosynthetic cotyledons (only the PEF seedling type) is higher in the Neotropical localities (mean ± SE = 49.5 ± 2.2) than in the Paleotropical ones (35.3 ± 1.3; Table 1), which is a quite significant difference (Mann-Whitney $U = 20.0$, $P = 0.017$). The second principal component, which explained 10.6% of variance among localities, showed a strong variation of seedling type spectra within regions. For example, Venezuela tends to be isolated from the rest of the Neotropical sites due to its high frequency

of PEF seedling type, and Indonesia tends to be isolated from the rest of the Paleotropical sites because of its high frequency of CER and CHR seedling types (Fig. 8, Table 1).

DISCUSSION

Ecological correlates and adaptive significance of seedling types—Hladik and Miquel (1990) suggested that the variety of morphological structures and physiological adaptations in seedling development is related to the heterogeneous structure of tropical forests, although few studies have demonstrated such association. Popma and Bongers (1988) showed that PEF seedlings generally grew faster than seedlings with other types when they were exposed to increased light. Strauss-Debenedetti and Bazzaz (1991), working with congeneric species of Moraceae (s.l.), found that PEF seedlings have higher maximum photosynthetic rates than CHR seedlings. Our results reveal the predominance of the PEF and CHR seedling types at Los Tuxtlas, which may suggest that these two particular types confer advantages to seedling survival and growth in the forest regeneration mosaic. The lack of association between species seedling type and species stratum position (canopy and subcanopy) suggests that the functional role of seedling morphology at our study site is unlinked to plant size maturation (but see Thomas and Bazzaz, 1999).

Among species with PEF seedlings there seems to be a wide range of morphophysiological behaviors to cope with contrasting understory light regimes (e.g., Kitajima, 1992). Although this seedling type is frequently associated with gap-dependent species (Martínez-Ramos and Samper, 1998), PEF seedlings also occur in species that establish and grow in the shaded understory, as in some taxa of Melastomataceae, Moraceae, and Rubiaceae (Ellison et al., 1993; Metcalfe and Grubb, 1995). At Los Tuxtlas, it was found that PEF seedlings of *Psychotria* species (Rubiaceae) showed a wide range of shade tolerance positively related to seed size variation, both within and among species (Paz, 1999). In fact, within the PEF seedling group in our study, persistent trees and lianas had bigger seeds than pioneer trees (Fig. 2b). Nevertheless, Kitajima (1992) suggested that foliaceous photosynthetic cotyledons enable the plants to use rich light resources found in forest gaps. We distinguished that pioneer species, which are strong light-demanding trees, had the smallest seeds among species with PEF seedlings (Fig. 2b), like *Cecropia obtusifolia* (Cecropi-
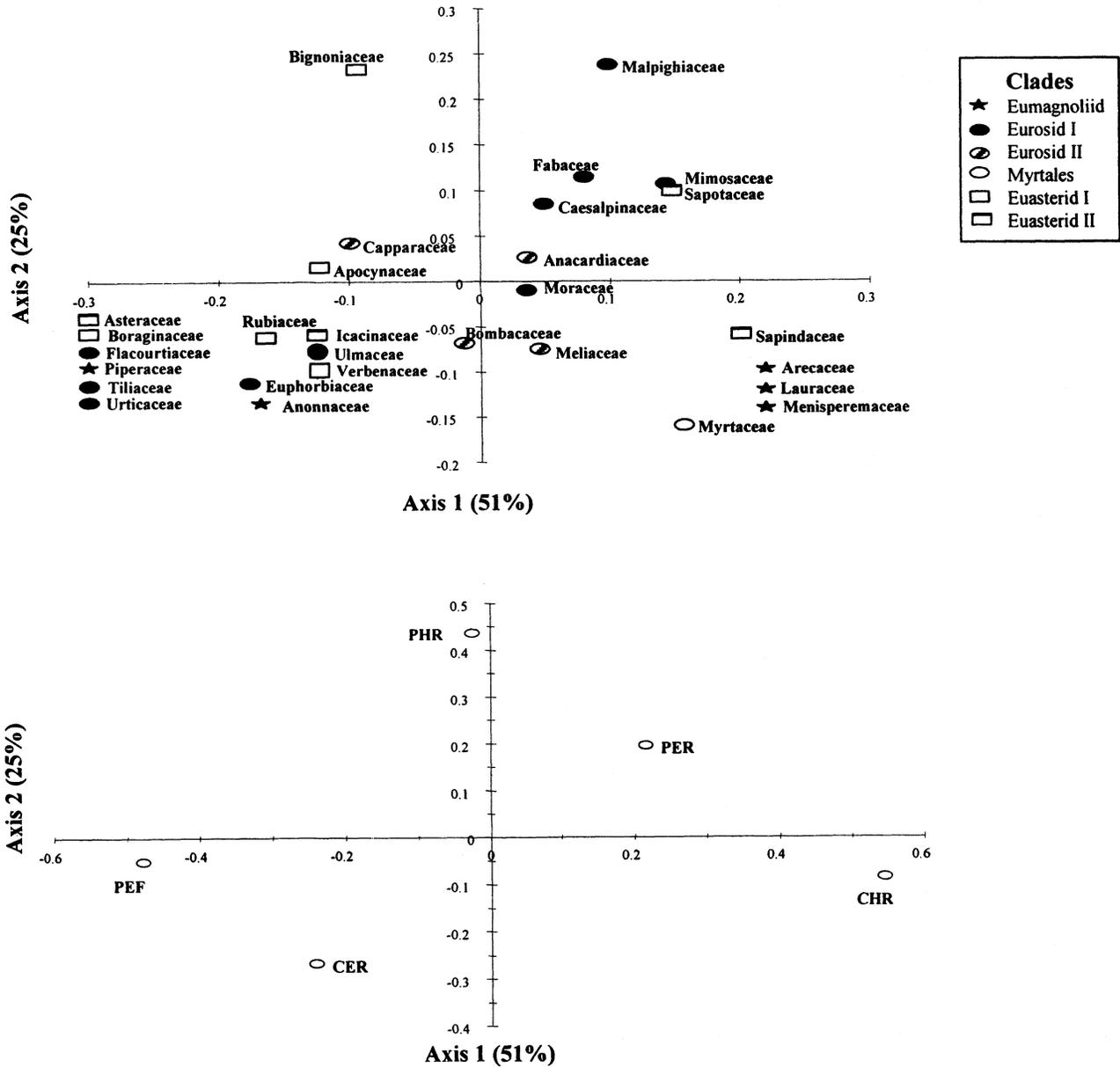
Fig. 6. Correspondence analysis ordination of families (top) and seedling types (bottom) considering tree and liana species from the Los Tuxtlas rain forest, Mexico. Only families with three or more species are included. Assignation of families to high-order clades was based mainly on Soltis, Soltis, and Chase (1999). In the top panel, some families had the same first axis score and those are listed in alphabetic order. According to the Cronquist (1981) scheme, stars indicate species in the subclass Magnoliidae, circles illustrate those species in the subclass Rosidae, and squares show those species in the subclass Asteridae.

aceae), which is the dominant species in natural gaps at Los Tuxtlas (Alvarez-Buylla and Martínez-Ramos, 1992). According with our results, dispersal capacity of species with PEF seedlings, in general (Fig. 3a), and in the pioneer species in particular (Fig. 4b), has evolved in association with animal and abiotic dispersal vectors.

The CHR seedling type is presumably related to plant life histories adjusted to light-limited environments (Foster, 1986; but see Kelly and Purvis, 1993). It has been found that seedling survival in the shade increases with seed size (e.g., Leishman and Westoby, 1994; Saverimuttu and Westoby, 1996; Paz, Mazer, and Martínez-Ramos, 1999). Furthermore, bigger seeds produce more vigorous seedlings that better withstand physical and biotic damages (Clark and Clark, 1991). At Los Tuxtlas,

we found that species with the CHR seedling type had the largest seed size (see Fig. 2a); most of these species develop in the shade, including the most abundant arboreal species at Los Tuxtlas, the upper-canopy tree *Nectandra ambigens* (Lauraceae), the mid-canopy *Pseudolmedia oxyphyllaria* (Moraceae), and the understorey palm *Astrocaryum mexicanum* (Dirzo, Ibarra-Manríquez, and Sánchez-Garduño, 1997; Martínez Ramos, 1997; Martínez Ramos, Ibarra-Manríquez, and Meave, 1997). In the same forest, tree species with seedlings having cotyledons functioning as reserve organs were significantly overrepresented in the advance regeneration community; meanwhile, species with PEF seedlings were dominant in the seed rain and in the newborn seedling community (Martínez-Ramos and Soto-Castro, 1993).
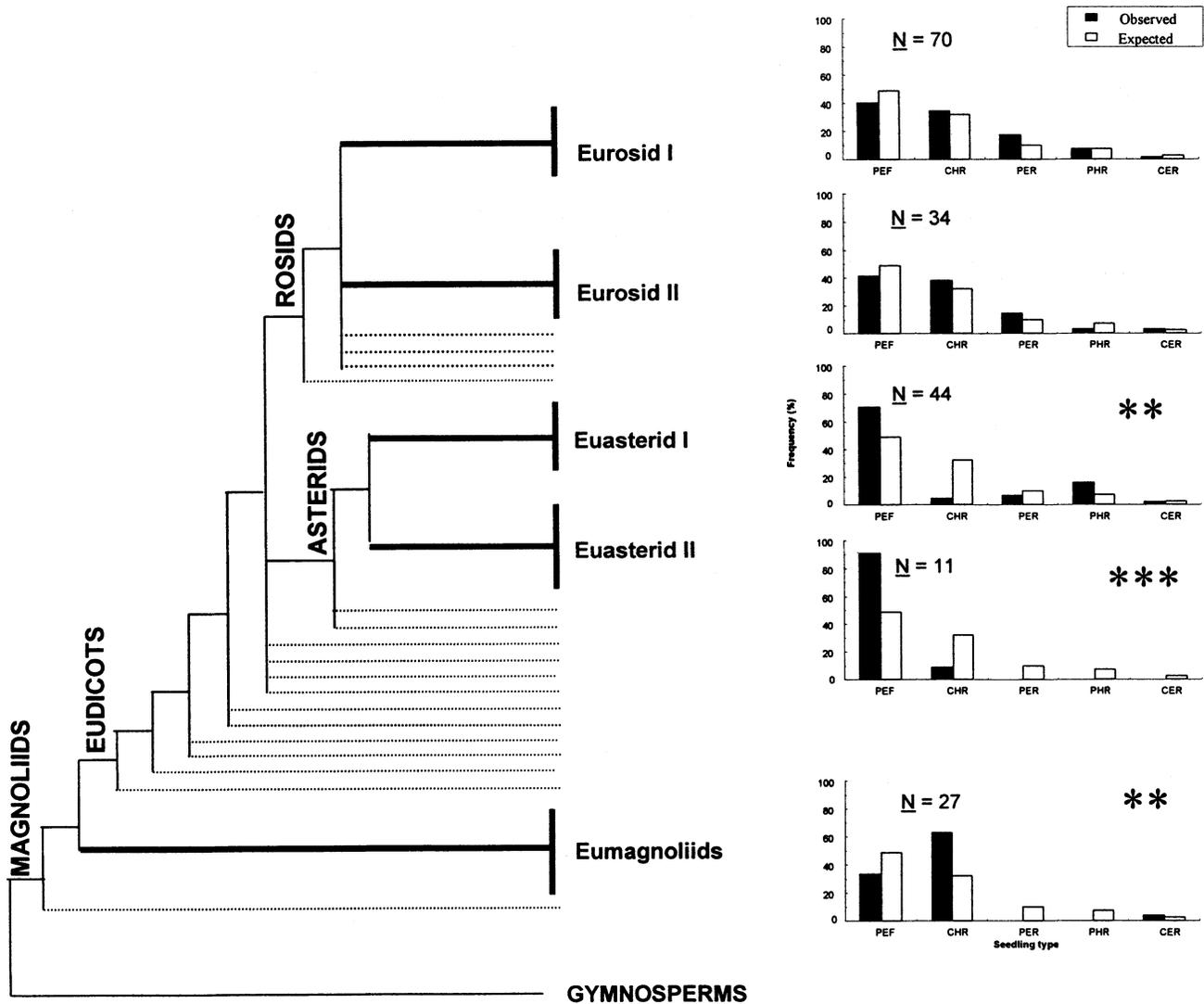
Fig. 7.   Angiosperm phylogenetic tree (modified from Soltis, Soltis, and Chase, 1999) and seedling type spectrum at Los Tuxtlas rain forest, Mexico. For each major clade, the seedling type spectrum of each clade was contrasted with that of the whole species sample ($N = 210$). After χ^2 tests, significant differences are indicated by ** ($P < 0.005$) or *** ($P < 0.001$). Broken lines indicate taxon (orders) not matched with Rosid and Asterid clades, within Eudicots, or with Eumagnoliids within Magnoliids.

Large seeds, however, are constrained to disperse near the neighborhood of maternal plants, where the probability of landing in a shaded site is high (Howe and Smallwood, 1982; Fenner, 1985; González-Méndez, 1995). The dominance of the animal dispersal syndrome in species with CHR seedlings (Fig. 3a) suggests that zoochory is important for the movement of large seeds outside the maternal neighborhood, where high mortality risks associated with density-dependent factors may occur (e.g., Clark and Clark, 1984).

Few systematic studies exist on seed germination and seedling establishment for liana species with an ecological approach. In our study, lianas and trees did not differ in seedling type frequencies. Garwood (1996) predicted the existence of "a few" liana species with the CER seedling type in tropical communities; however, no liana species at Los Tuxtlas had CER seedlings in our sample. On the other hand, the family Bignoniaceae is a very widespread and diversified taxonomic plant group both in species and seedling types, and most of the liana species with PHR seedlings belong to this family.

Discarding this family, general trends in seedling types in liana species might not be so different from other plant species at Los Tuxtlas forest. The same is correct for the Gabon case (Hladik and Miquel, 1990), as we did not find significant differences in seedling type frequencies between tree and liana species in their data ($\chi^2 = 6.7$, df $= 4$, $P > 0.10$). Finally, there is a general view that most lianas are light-dependent plants (Putz, 1984; Hegarty and Caballé, 1991). According with this view we would expect that PEF seedling type must be predominant among lianas species. The fact that our results did not support this expectancy suggests that seedling type is uncoupled to light-dependence of lianas or that among liana species there could be a wide range of regeneration strategies as takes place among tree species.

Phylogenetic patterns—Our taxonomic analysis showed that seedling type is a trait with strong phylogenetic inertia at the genus, family, and even higher order clades. In some families, like the magnoliid families Arecaceae, Lauraceae, and

(a)

(b)
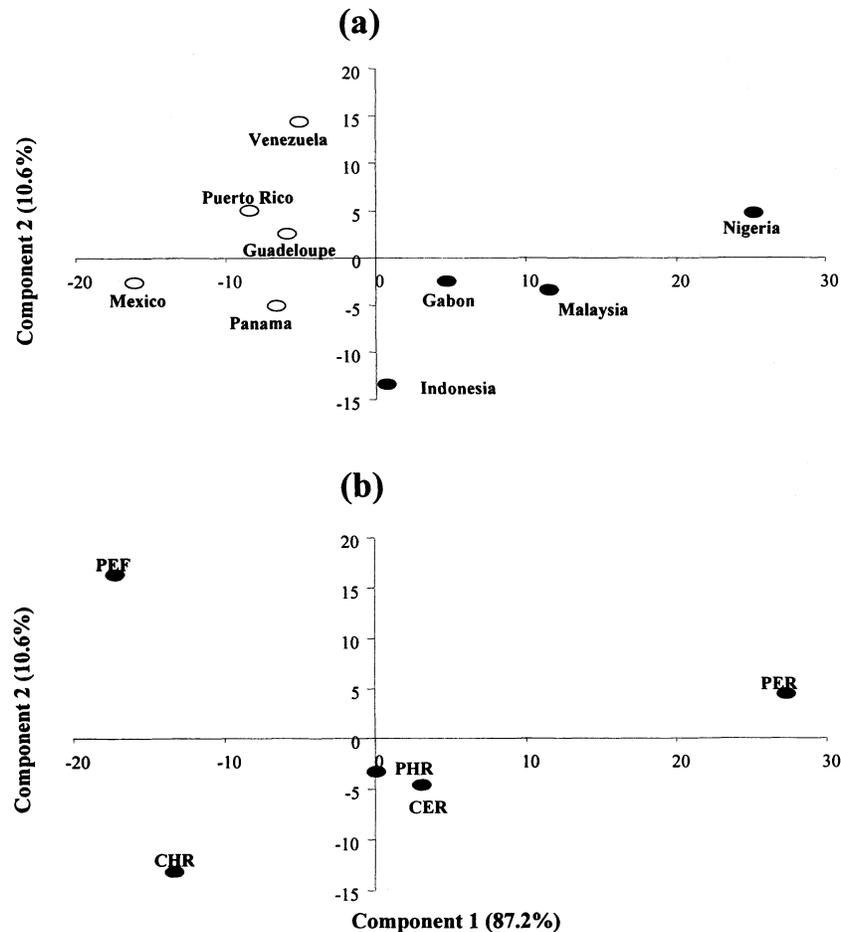
Fig. 8. Principal components analysis of rain forest localities (a) and seedling types (b) of woody species from nine rain forests around the world. In (a), Paleotropical sites are indicated by filled circles and Neotropical localities by open circles.

Piperaceae, all species have the same seedling type or, at least, the same dominant type (e.g., Euphorbiaceae, Rubiaceae, or Sapotaceae), and congeneric species shared the same seedling type in 86% of the study genera. One remarkable result was that the relative frequency of families composed of species with same seedling type was much higher than that expected by random, even for the most speciose families. Overall, these results suggest that the evolution of the initial seedling morphology in tropical rain forest woody plants, as described by the position and function of cotyledons, is a trait that may be constrained at taxonomic levels higher than family and thus, that phylogenetic inertia exists in the evolution of this trait (e.g., de Vogel, 1980; Garwood, 1996). In other words, from an evolutionary perspective seedling type seems to be a very conservative trait. However, some examples of apparent evolutionary radiation or convergence, associated with a diversification in morphophysiological traits of seedlings, were also noted. For example, families of different clades shared similar frequency of seedling types (Fig. 6), and some families showed a highly diversified seedling type spectrum. Similar trends were noted at Gabon, Africa (Hladik and Miquel, 1990), where a different rain forest flora exists.

Assuming Asterids as the most recent clade and Magnoliids as the most ancient one, our phylogenetic analysis based on the Los Tuxtlas data suggests that PEF, CHR, and CER seedlings could be the first seedling types appearing in the evo-

lution of woody angiosperms that inhabit tropical rain forest and that PER and PHR seedling types arose later with the Rosids (Fig. 7). It seems that an important change has occurred along this apparent evolutionary trend. So, while species with seedlings with cotyledons functioning as reserve storage organs had declined, those with photosynthetic cotyledons had increased. The relative species frequency of the PEF seedling type in the Eumagnoliids was <35% and it was >90% in the Euasterids II. In contrast, the other seedling types have changed in the opposite way, particularly the CHR seedling type that passed from >60% in the Eumagnoliids to ~10% in the Euasterids II (Fig. 7). To gain a better understanding of the evolution of seedling functional traits we need to expand this type of analysis to other rain forest floras and to study the particular evolutionary routes by which these apparent evolutionary changes occurred.

Seedling type spectrum in tropical rain forests—The seedling type spectrum at Los Tuxtlas was dominated by species with PEF and CHR seedlings. With the exception of the Nigeria site, this result is similar to those found in other Neotropical and Paleotropical rain forest localities studied to date (Table 1). In contrast, species frequency of the PER seedling type at Los Tuxtlas is the lowest in these localities. Further studies will clarify whether this low frequency is due to ecological, biogeographical, or phylogenetic reasons.

Also, CER seedling type in Los Tuxtlas was among the lowest in the compared localities (Table 1). We need to point out that taxonomic occurrence of this seedling type is not negligible as it can be found in 14 plant families, and 2 of these families (Annonaceae and Euphorbiaceae) have an intercontinental forest occurrence. Hladik and Miquel (1990) reported nine CER seedling species at Makokou forest, Gabon, where these species exhibit high population densities, although their seeds have poor germination and the seedlings fail to develop properly under nursery conditions. At Los Tuxtlas, the understory tree *Faramea occidentalis* (Rubiaceae) has this syndrome. It may reach high densities of >70 individuals ≥0.5 m in height per hectare (Bongers et al., 1988) and have seeds that delay germination >3 mo. The other four species with the CER seedling type germinate rapidly and are very uncommon in Los Tuxtlas forest (e.g., <9 individuals/ha; Bongers et al., 1988).

Data presented in Table 1 reveal that Neotropical localities generally have higher frequencies of PEF and CHR seedling types, whereas their Paleotropical counterparts show high values in PHR, CER, and PER seedling categories. This pattern was statistically significant and it was mostly due to the high number of species with PEF seedling type in the Neotropical sites (Table 1). One line of evidence to explain this pattern could be the differences in forest dynamics among tropical localities. For example, among tropical rain forests there is a great variation in forest turnover rates (Phillips and Gentry, 1994), and the frequency of PEF seedling type could rise as the number of favorable sites for establishment of climbing and gap-dependent tree species increases. In this context, one open question is whether the frequency of PEF seedling type could be positively related to forest turnover rate.

Also, biogeographic differences in seedling type spectra may have a relationship to the influence of taxonomic affinities among forest localities. This is plausible because, as discussed previously, the seedling type spectrum is greatly influenced by the species phylogenetic relations. Taxonomic affinities among Neotropical forests are illustrated by the fact that of the 120 genera listed by Garwood (1983) on Barro Colorado Island (Panama), almost half are present also at Los Tuxtlas. Also, Neotropical forests tend to have similar family composition (Gentry, 1988, 1990; Martínez-Ramos, 1994). In contrast, Neo- and Paleotropical forests share ~30% of genera of woody plants ≥2.5 cm diameter at breast height recorded in a large set of 0.1-ha plots (Gentry, 1988).

Concluding remarks—This and other studies show that the seedling initial morphology, classified as discrete seedling types, has an interpretable ecological meaning. Seedling type is linked with the dispersal capacity and the regenerative strategy of species. This association does not depend on the plant life form (liana or tree) or the position that species occupy as mature plants in the forest canopy. The evolutionary history producing the present seedling type spectrum, however, must be explored among old taxonomic lineages as seedling morphology type has strong phylogenetic inertia among species of the same family or genus.

To advance our understanding of the ecological and evolutionary significance of the early life cycle traits of rain forest plants, it is necessary to develop comparative studies on the ecological processes during establishment of many plant species (Garwood, 1996), particularly of plant life forms scarcely studied (e.g., climbers). Based on our results, we think that

the categorization of seedlings based on function and position of cotyledons is of small help in the study of recent evolution of seedling functional morphology. To improve our knowledge on this issue, we need to understand better the variation and ecological role of seedling traits such as seedling size, rate of developmental stages, resource allocation among seedling organs, amount and quality of maternal reserves, or root, stem, and leaf morphology and function.

LITERATURE CITED

ALVAREZ-BUYLLA, E., AND M. MARTÍNEZ-RAMOS. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84: 314–325.

ALVAREZ-BUYLLA, E., AND M. MARTÍNEZ-RAMOS. 1992. The demography and allometry of *Cecropia obtusifolia,* a Neotropical pioneer tropical tree: an evaluation of the climax-pioneer paradigm for a tropical rain forest. *Journal of Ecology* 80: 275–290.

ANGEVINE, M. W., AND B. F. CHABOT. 1979. Seed germination syndromes in higher plants. *In* O. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven [eds.], Topics in plant population biology, 188–206. Columbia University Press, New York, New York, USA.

AUGSPURGER, C. K. 1984. Light requirements of Neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72: 777–795.

BARRERA, T. E. 1985. Identificación de plántulas de algunas especies arbóreas del bosque de niebla. *Perez-Arbelaezia* 1: 39–95.

BHATTACHARYYA, B., AND B. M. JOHRI. 1998. Flowering plants: taxonomy and phylogeny. Springer-Verlag, Narosa Publishing House, New York, New York, USA.

BONGERS, F., J. POPMA, J. MEAVE, AND J. CARABIAS. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* 74: 55–80.

CLARK, D. A., AND D. B. CLARK. 1984. Spacing dynamics of a tropical rain forest trees: evaluation of the Janzen-Connell model. *American Naturalist* 124: 769–788.

CLARK, D. A., AND D. B. CLARK. 1991. The impact of physical damage on canopy tree regeneration in a tropical rain forest. *Journal of Ecology* 79: 447–458.

CRAWLEY, M. J. 1993. GLIM for ecologists. Blackwell Scientific, Oxford, UK.

CRONQUIST, A. 1981. An integrated systems of classification of flowering plants. Columbia University Press, New York, New York, USA.

DEL AMO, S. 1979. Clave para plántulas y estados juveniles de especies primarias de una selva alta perennifolia en Veracruz, México. *Biótica* 4: 59–108.

DE VOGEL, E. F. 1980. Seedlings of dicotyledons. Structure, development, types. Descriptions of 150 woody Malesian taxa. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

DIRZO, R., G. IBARRA-MANRÍQUEZ, AND C. SÁNCHEZ-GARDUÑO. 1997. *Nectandra ambigens* (laurel chilpatillo). *In* E. González-Soriano, R. Dirzo, and R. C. Vogt [eds.], Historia natural de Los Tuxtlas, 124–129. Instituto de Biología e Instituto de Ecología, Universidad Nacional Autónoma de México y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, S y G editores, México, D. F., México.

DUKE, J. A. 1965. Keys for the identification of seedlings of some prominent woody species in eight forest types in Puerto Rico. *Annals of the Missouri Botanical Garden* 52: 314–350.

DUKE, J. A. 1969. On tropical seeds, seedlings, systems, and systematics. *Annals of the Missouri Botanical Garden* 56: 125–161.

DUKE, J. A., AND R. M. POLHILL. 1981. Seedlings of Leguminosae. *In* R. M. Polhill and P. H. Raven [eds.], Advances in legume systematics, 941–949. Royal Botanical Gardens, Kew, Richmond, Surrey, UK.

ELLISON, A. M., J. S. DENSLOW, B. A. LOISELLE, AND M. D. BRENES. 1993. Seed and seedling ecology of Neotropical Melastomataceae. *Ecology* 74: 1733–1749.

EZCURRA, E. 1992. Orden. Versión 2.0. Instituto de Ecología, Universidad Nacional Autónoma de México, México.

FENNER, M. 1985. Seed ecology. Chapman and Hall, New York, New York, USA.

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

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

GARWOOD, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs* 53: 159–181.

GARWOOD, N. C. 1996. Functional morphology of tropical tree seedlings. *In* M. D. Swaine [ed.], The ecology of tropical forest tree seedlings, 59–129. Man and the Biosphere series, vol. 17. UNESCO, Paris and Parthenon, Paris, France.

GENTRY, A. H. 1988. Change in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75: 1–34.

GENTRY, A. H. [ED.]. 1990. Four Neotropical forests. Yale University Press, New Haven, Connecticut, USA.

GONZÁLEZ-MÉNDEZ, M. 1995. Consecuencias ecológicas de la variación interespecífica en las curvas de dispersión de semillas en una selva alta perennifolia. B.Sc. thesis, Universidad Nacional Autónoma de México, México.

GONZÁLEZ-SORIANO, E., R. DIRZO, AND R. C. VOGT [EDS.]. 1997. Historia natural de Los Tuxtlas. Instituto de Biología e Instituto de Ecología, Universidad Nacional Autónoma de México and Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, S y G editores, México, D. F., México.

GRUBB, P. J., AND D. J. METCALFE. 1996. Adaptation and inertia in the Australian tropical lowland rain-forest flora: contradictory trends in intergeneric and intrageneric comparisons of seed size in relation to light demand. *Functional Ecology* 10: 512–520.

HARPER, J. L. 1977. Population biology of plants. Academic Press, London, UK.

HEGARTY, E. E., AND G. CABALLÉ. 1991. Distribution and abundance of vines in forest communities. *In* F. E. Putz and H. E. Mooney [eds.], The biology of vines, 313–335. Cambridge University Press, Cambridge, UK.

HLADIK, A., AND S. MIQUEL. 1990. Seedling types and plant establishment in an African rain forest. *In* K. S. Bawa and M. Hadley [eds.], Reproductive ecology of tropical forest plants, 261–282. Man and the Biosphere series, vol. 7. UNESCO, Paris and Parthenon, Paris, France.

HOWE, H. F., AND W. M. RICHTER. 1982. Efects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. *Oecologia* 53: 347–351.

HOWE, H. F., AND J. SMALLWOOD. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

IBARRA-MANRÍQUEZ, G., AND S. SINACA-COLÍN. 1995. Lista florística comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México. *Revista de Biología Tropical* 43: 75–115.

IBARRA-MANRÍQUEZ, G., AND S. SINACA-COLÍN. 1996a. Estación de Biología Tropical "Los Tuxtlas," Veracruz, México: lista florística comentada (Mimosaceae a Verbenaceae). *Revista de Biología Tropical* 44: 41–60.

IBARRA-MANRÍQUEZ, G., AND S. SINACA-COLÍN. 1996b. Lista comentada de plantas de la Estación de Biología Tropical "Los Tuxtlas," Veracruz, México (Violaceae a Zingiberaceae). *Revista de Biología Tropical* 44: 427–447.

IBARRA-MANRÍQUEZ, G., M. MARTÍNEZ-RAMOS, R. DIRZO, AND J. NÚÑEZ-FARFÁN. 1997. La Vegetación. *In* E. González-Soriano, R. Dirzo, and R. C. Vogt [eds.], Historia natural de Los Tuxtlas, 61–85. Instituto de Biología e Instituto de Ecología, Universidad Nacional Autónoma de México y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, S y G editores, México, D. F., México.

JUDD, W. S., S. C. CAMPBELL, E. A. KELLOG, AND P. F. STEVENS. 1999. Plant systematics: a phylogenetic approach. Sinauer, Sunderland, Massachusetts, USA.

KELLY, C. K., AND A. PURVIS. 1993. Seed size and establishment conditions in tropical trees: on the use of taxonomic relatedness in determining ecological patterns. *Oecologia* 94: 356–360.

KITAJIMA, K. 1992. Relationship between photosynthesis and thickness of cotyledons for tropical tree species. *Functional Ecology* 6: 582–589.

KITAJIMA, K. 1996. Cotyledon functional morphology, patterns of seed reserve utilization and regeneration niches of tropical tree seedlings. *In* M. D. Swaine [ed.], The ecology of tropical forest tree seedlings, 193–210.

Man and the Biosphere series, vol. 17. UNESCO, Paris and Parthenon, Paris, France.

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

LEISHMAN, M. R., M. WESTOBY, AND E. JURADO. 1995. Correlates of seed size variation: a comparison among five temperate floras. *Journal of Ecology* 83: 517–530.

MARTÍNEZ-RAMOS, M. 1994. Regeneración natural y diversidad de especies arbóreas en selvas húmedas. *Boletin de la Sociedad Botánica de México* 54: 179–224.

MARTÍNEZ-RAMOS, M. 1997. *Astrocaryum mexicanum* (chocho, chichón). *In* E. González-Soriano, R. Dirzo, and R. C. Vogt [eds.], Historia natural de Los Tuxtlas, 92–97. Instituto de Biología e Instituto de Ecología, Universidad Nacional Autónoma de México y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, S y G editores, México, D. F., México.

MARTÍNEZ-RAMOS, M., E. ALVAREZ-BUYLLA, AND J. SARUKHÁN. 1989. Tree demography and gap dynamics in a tropical rain forest. *Ecology* 70: 355–358.

MARTÍNEZ-RAMOS, M., AND A. SOTO-CASTRO. 1993. Seed rain and advanced regeneration in a tropical rain forest. *Vegetatio* 107/108: 299–318.

MARTÍNEZ-RAMOS, M., G. IBARRA-MANRÍQUEZ, AND J. MEAVE. 1997. *Pseudolmedia oxyphyllaria* (tomatillo). *In* E. González-Soriano, R. Dirzo, and R. C. Vogt [eds.], Historia natural de Los Tuxtlas, 138–143. Instituto de Biología e Instituto de Ecología, Universidad Nacional Autónoma de México y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, S y G editores, México, D. F., México.

MARTÍNEZ-RAMOS, M. AND C. SAMPER. 1998. Tree life history patterns and forest dynamics: a conceptual model for the study of plant demography in patchy environments. *Journal of Sustainable Forestry* 6: 85–125.

METCALFE, D. J., AND P. J. GRUBB. 1995. Seed mass and light requirements for regeneration in Southeast Asian rain forest. *Canadian Journal of Botany* 73: 817–826.

MIQUEL, S. 1987. Morphologie fonctionnelle de plantules d'espèces forestières du Gabon. *Bulletin du Muséum National d'Histoire Naturelle, 4e série, section B, Adansonia* 9: 101–121.

NG, F. S. P. 1978. Strategies of establishment in Malayan forest. *In* P. B. Tomlinson and M. H. Zimmermann [eds.], Tropical trees as living systems, 129–162. Cambridge University Press, Cambridge, UK.

PAZ, H. 1999. Sobre el significado ecológico y evolutivo de la masa de la semilla: un análisis comparativo para ocho especies del género Psychotria, en Los Tuxtlas, Veracruz, México. Ph.D. dissertation, Universidad Nacional Autónoma de México, México, D. F., México.

PAZ, H., S. J. MAZER, AND M. MARTÍNEZ-RAMOS. 1999. Seed mass, seedling emergence and environmental factors in seven rain forest *Psychotria* (Rubiaceae). *Ecology* 80: 1594–1606.

PHILLIPS, O. L., AND A. H. GENTRY. 1994. Increasing turnover through time in tropical forests. *Science* 263: 954–958.

POPMA, J., AND F. BONGERS. 1988. The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* 75: 625–632.

PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65: 1713–1724.

SAVERIMUTTU, T., AND M. WESTOBY. 1996. Seedling longevity under deep shade in relation to seed size. *Journal of Ecology* 84: 681–689.

SILVERTOWN, J., M. FRANCO, I. PISANTY, AND A. MENDOZA. 1993. Comparative plant demography. Relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *Journal of Ecology* 81: 465–476.

SOLTIS, P., D. E. SOLTIS, AND M. W. CHASE. 1999. Angiosperm phylogeny inferred fro multiple genes as a tool for comparative biology. *Nature* 402: 402–404.

STRAUSS-DEBENEDETTI, S., AND F. A. BAZZAZ. 1991. Plasticity and acclimation to light in tropical Moraceae of different successional positions. *Oecologia* 87: 377–387.

SWAINE, M. D., AND T. C. WHITMORE. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75: 81–86.

THOMAS, S. C., AND F. A. BAZZAZ. 1999. Asymptotic height as predictor of photosynthetic characteristics in Malaysian rain forest trees. *Ecology* 80: 1607–1622.