

DEVELOPMENTAL STRATEGY OR IMMEDIATE RESPONSES IN LEAF TRAITS OF TROPICAL TREE SPECIES?

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We asked whether the ability of individual plants to adjust leaf traits during ontogeny reflected immediate morphological means of responding to current light availability or was consistent with a developmental strategy to meet predictable future light conditions. We determined leaf mass per unit area (specific leaf mass, SLM), leaf area, toughness, and water content of seedlings, juveniles, and adults of eight nonpioneer tropical tree species of different maximum mature heights ranging from 8 to 40 m. For SLM and leaf area, immediate responses to environmental conditions, reported as the ratio of leaf traits in sun and shade environments (leaf plasticity), were similar for seedlings, juveniles, and adults of all species irrespective of maximum mature height. For toughness and water content, leaf plasticity at different ontogenetic stages depended on species identity. To facilitate comparisons across species, developmental changes were reported as the correlations between the ratio in leaf traits for three ontogenetic stages (developmental leaf change) and maximum mature height. Tall species showed greater change in SLM and leaf area from seedling to adult stages than short species, as might be expected of taxa that experience more heterogeneous light environments during their lives. Leaf traits changed in response to current light levels during ontogeny, but the magnitude of the response is related to the adult habitat of a species.

Keywords: Los Tuxtlas, Mexico, rain forest, specific leaf area, tropical tree growth.

Introduction

Values of a variety of leaf traits of tropical tree species change during ontogenetic development, coinciding with increases in light availability as individuals increase in size (Coleman et al. 1994; Davies et al. 1998). Seedlings and juveniles of the shaded understory undergo morphological and physiological adjustments when gaps created by tree falls or branch falls suddenly expose them to increased light levels (Bongers et al. 1988a; Agyeman et al. 1999; Poorter 2001). Plants in high-light conditions have smaller leaves with higher leaf mass per unit area (specific leaf mass, SLM), higher water content, and greater toughness than plants in low-light environments (Parkhurst and Loucks 1972; Bongers and Popma 1988; Witkowski and Lamont 1991; Percy and Sims 1994). Quantitative changes in leaf traits are in part responsible for increased growth rates under higher light levels (King 1994). Few studies, however, explore the changes in leaf traits that result from the interaction of ontogeny, current light availability, and potential light availability that species are likely to experience as adults (Thomas and Bazzaz 1999; Rijkers et al. 2000). An open question is whether changes in dimensions of leaf traits reflect immediate adjustments to local conditions or a developmental strategy that

anticipates the future conditions likely to be encountered during the ontogeny of a tree.

Plants may adjust leaf traits of photosynthetic importance to the immediate light conditions that they experience as they grow, or changes may be strategic, increasing the chance that individuals can adjust, if necessary, to conditions that they are likely to experience for most of their lives. As an example of a phenotypic response to immediate conditions, Percy and Sims (1994) show in the tropical herb *Alocasia macrorrhiza* (L.) Schott (Araceae) that SLM doubles in contrasting light levels (from 15 to 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$). As an example of strategic response to environmental conditions through developmental changes, Winn (1996b) found that individuals of *Dicerandra linearifolia* (Ell.) Benth. (Lamiaceae) changed SLM from 4.5 to 7.5 mg cm^{-2} from early to late ontogenetic stages even when environmental conditions usually associated with these changes were not present. In addition, comparative evidence indicates that tree species of different maximum mature heights, when exposed to different light levels, modulate leaf area as part of ontogenetic development. Tall species also may be expected to have smaller, thicker, and heavier (higher SLM) leaves at the adult stage than at the seedling stage, in response to the higher light levels they experienced as they gain height. For example, in Malaysia juveniles of tall species have larger leaves than conspecific adults, while juveniles of short species have smaller leaves than conspecific adults (Thomas and Ickes 1995; $N = 51$ species). Within this sample, short species show less change in SLM from juvenile to adult than tall species (Thomas and Bazzaz 1999; $N = 28$ species), perhaps reflecting the more similar light environments shared by juveniles

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and adults of short species as compared with juveniles and adults of tall species. What remains to be tested is whether these and other adjustments are immediate phenotypic responses to light environments of a given ontogenetic stage or part of a strategy that has evolved in response to predictable changes in light environment throughout development.

Here we ask if seedlings, juveniles, and adults of eight late-successional tree species change leaf traits in response to immediate light level in sun or shade or if this response depends on their maximum mature height, reflecting programmed developmental change. Immediate response to environmental conditions is evaluated using mean values of leaf traits and leaf plasticity, as estimated by the ratio of values of the same leaf trait in sun and shade. To assess developmental strategy to meet future light levels, we evaluated the correlations between the ratios of seedling and adult, seedling and juvenile, and juvenile and adult leaf traits (developmental leaf change) and maximum mature height. The hypothesis of immediate responses will be supported if species show (1) leaves in sunny environments with higher SLM, lower leaf area, higher water content, and greater toughness than leaves in shade environments and (2) similar plasticities for leaf traits. Alternatively, (3) leaf change may reflect programmed changes related to maximum mature height of a species, in which immediate responses and plasticity play a smaller role. There is also the possibility, reflecting phylogeny or other possible consistent life-history challenges, of (4) developmental leaf change unrelated to maximum mature height. This might be expressed as taxonomic differences in ratios of leaf traits from one ontogenetic stage to another without association with maximum mature height.

Material and Methods

Study Site

This study was conducted in Los Tuxtlas Biological Station (LTBS) in the state of Veracruz, southeast Mexico (18°30'N and 95°03'W), and in an experimental planting located in the Cooperative of Lázaro Cardenas close to LTBS. LTBS lies within a reserve of 640 ha of lowland tropical rain forest that constitutes the northernmost rain forest in the Neotropics; the Cooperative of Lázaro Cardenas is located in the southwest corner of the reserve. Soils are sandy loams, classified as vitric andosols (FAO/UN 1975 in Soto-Esparza 1976). Mean annual temperature is 27°C, and mean annual rainfall is 4900 mm. The dry season extends from March to May and the rainy season from June to February. The forest has a 35-m-tall closed canopy. *Nectandra ambigens* (Blake) C.K. Allen (Lauraceae) is the most common species in the canopy, while *Pseudolmedia oxyphyllaria* Donn. Sm. (Moraceae) and *Astrocaryum mexicanum* Liebm. (Arecaceae) are abundant in the midcanopy and understory, respectively (Bongers et al. 1988b). Field crops, pastures, and small forest remnants surround this forest reserve. The experimental planting is located within a 25-ha parcel of former forest that was felled in 1978 and used as agricultural land for 4 yr and for cattle ranching for 15 yr. The secondary forest has a 15-m-tall canopy of pioneer species: *Cecropia obtusifolia* Bertol. (Cecropiaceae), *Heliocarpus appendiculatus* Turcz. (Tiliaceae),

Bursera simaruba (L.) Sarg. (Burseraceae), and *Cedrela odorata* L. (Meliaceae). Mean (\pm SE) instantaneous measurement of photon flux density (PFD; Li-Cor LI-189 quantum sensor light meter) in the dry season in the secondary forest at 1.5 m from the forest floor at midday was $22 \pm 9 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($N = 75$; max. 50 and min. 10), while in the open pasture it was $1948 \pm 219 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($N = 11$; max. 2227 and min. 1730). Our secondary forest measures for all light were comparable to measures for photosynthetically relevant light (ca. $\leq 10 \mu\text{mol m}^{-2} \text{s}^{-1}$) of Chazdon and Fetcher (1984) in mature Costa Rican rain forest.

Sampling

In 1999, eight nonpioneer tree species, reflecting a range of maximum mature heights, that regenerate in shade or small canopy gaps were chosen from the experimental planting (table 1). This planting was created in 1997 in former pastures and secondary vegetation close to the Cooperative of Lázaro Cardenas. Species chosen from the experimental planting were those with a sufficient sample of seedlings growing under contrasting light levels in open pasture and in dense secondary vegetation, reflecting sun and shade environments.

Fully expanded, undamaged sun and shade leaves of all species in three ontogenetic stages (seedling, juvenile, and adult) were sampled in November 1999 from at least six individuals at the seedling and juvenile stages and three to six individuals at the adult stage of each species. Seedlings were < 1.3 cm diameter at the base and < 1.0 m high, except *Licaria velutina* (≤ 1.21 m height); juveniles were < 3.5 cm diameter at breast height (DBH; BH = 1.5 m) and 2.5 m tall, except *Nectandra* (≤ 8.9 cm DBH and 4 m tall). Adults were reproductive individuals ranging in DBH from 16 to 106 cm. A paucity of smaller seedlings of *Licaria* and juveniles of *Nectandra* required the larger cutoffs, because of very high growth rates for these species. For seedlings, individuals of all species were the same age.

Measures of leaf traits were taken on different plants to determine whether leaf characters were associated with low- and high-light environments (hereafter leaf environments). Adults and juveniles of all species were located in the LTBS reserve. Ten to 20 leaves of adult trees ($N = 3 - 6$ per species) were taken from the most exposed part of the canopy (sun environment) and at the very bottom of the crown (shade environment). Three to five leaves were taken from each branch selected. To produce comparable leaf ages among life stages, leaves were sampled just behind the new leaves. Juveniles were located in the understory (shade environment) and in canopy gaps with full vertical illumination (sun environment) inside the reserve. Ten leaves of each juvenile individual ($N = 3$ for each species) and five leaves of each seedling ($N = 3$ for each species) were sampled in sun and shade environments (a total of $N = 6$ for each species).

Leaves were measured within 2 h of collection. Leaf fresh mass was measured with a balance Pocket Pro 250-B (readability of 0.1 g), while fresh leaf area was measured by drawing the leaf perimeter on paper and determining area with a leaf area meter (Li-3100, Li-Cor, Lincoln, NE). Leaves were oven-dried to constant mass at 100°C to minimize water content and weighed to the nearest 0.001 g (Mettler PM 1200

Table 1
Range of Tree Heights and Regeneration Strategies of Eight Tropical Nonpioneer Tree Species Studied at Los Tuxtlas, Veracruz, Mexico

Species	Family	Key	Height (m) ^a	Regeneration strategy ^b
<i>Nectandra ambigens</i> (S.F. Blake) C.K. Allen	Lauraceae	Nect	20–40	Specialists of small gaps
<i>Brosimum alicastrum</i> Sw.	Moraceae	Bros	20–30	Specialists of small gaps
<i>Calophyllum brasiliense</i> Cambess.	Clusiaceae	Calo	20–30	Specialists of small gaps
<i>Pimenta dioica</i> (L.) Merr.	Myrtaceae	Pime	8–30	Specialists of small gaps ^c
<i>Eugenia inirebensis</i> P.E. Sánchez	Myrtaceae	Euge	8–15	Establishes in the shade ^c
<i>Licaria velutina</i> van der Werff	Lauraceae	Lica	10–15	Specialists of small gaps
<i>Amphitecna tuxtliensis</i> A.H. Gentry	Bignoniaceae	Amph	3–10	Establishes in the shade
<i>Pouteria rhynchocarpa</i> T.D. Penn.	Sapotaceae	Pout	3–8	Establishes in the shade

Note. Species are listed in order of maximum mature stature reported in the literature. Key refers to the word used to designate each species in figure 1. Nomenclature follows Ibarra-Manríquez and Sinaca (1995, 1996a, 1996b).

^a Ibarra-Manríquez and Sinaca 1995, 1996a, 1996b.

^b From Martínez-Ramos 1985; Popma et al. 1992, except as noted.

^c Martínez-Garza 2003.

balance). SLM is the leaf dry mass per unit fresh leaf area. Leaf water content was calculated on a fresh-mass basis [(leaf fresh mass – leaf dry mass)/leaf area], while leaf toughness was measured with a penetrometer (Choong et al. 1992).

Data Analysis

To test for the effect of species identity, sun or shade leaf environments, and ontogenetic stage (seedling, juvenile, and adult) on leaf traits, multivariate analysis of variance (MANOVA) was used. The mean of each leaf trait for five to 20 leaves for each individual was used in all analyses ($N = 18$ data points per species). To calculate leaf plasticity (the ratio of mean values of a trait in sun and shade environments), three pairs of individuals for each ontogenetic stage for each species were used ($N = 9$ data points per species). MANOVA was used to test for the effect of species identity and ontogenetic stage on plasticity of leaf traits. Univariate ANOVA tests were performed only after significant MANOVA results, to guard against Type I errors (Zar 1974). Tukey post hoc comparisons, conservative because they employ reduced degrees of freedom, were used to detect especially strong differences revealed by significant univariate analyses. Mean leaf traits and their plasticities were log-transformed to satisfy MANOVA assumptions. The mean leaf trait from sun and shade leaf environments of six individuals for each ontogenetic stage and each species was used in the developmental leaf change calculations; three ratios that correspond to the following transitions among ontogenetic stages were calculated to facilitate comparisons across species: (1) the ratio of seedling and adult leaf traits, (2) the ratio of seedling and juvenile leaf traits, and (3) the ratio of juvenile and adult leaf traits. To test the association of these three ratios with maximum mature height, Spearman rank correlations were performed with these variables transformed into ranks. Finally, mean leaf trait from sun and shade leaf environments and leaf plasticity of all leaf traits for each species were correlated with maximum mature height. Means are accompanied by standard errors throughout. All tests were performed with

STATISTICA, version 5.1 (StatSoft 1998). After introduction in table 1, species are referred to by genus.

Results

Immediate Responses of Leaf Traits

Mean leaf traits. Overall mean values for eight species pooling across leaf environments and three ontogenetic stages were as follows: SLM 76.49 ± 2.2 g m⁻², leaf area 51.59 ± 3.1 cm², toughness 120.4 ± 2 g, and water content 98.7 ± 3.3 g m⁻². Leaf traits differed by species, ontogenetic stage, and leaf environment (table 2). SLM ranged from 54.86 (*Amphitecna*) to 102.22 (*Pimenta*) g m⁻², leaf size ranged from 31.45 (*Pouteria*) to 144.51 cm² (*Licaria*), toughness ranged from 98.67 (*Brosimum*) to 141.5 g (*Amphitecna*), and water content ranged from 51.63 (*Pouteria*) to 129.81 g m⁻² (*Pimenta*). Post hoc Tukey tests revealed that adults showed significantly higher SLM, toughness, and water content than juveniles and seedlings. Juveniles showed significantly higher leaf area than adults and seedlings, which had comparable lower leaf areas (table 3). Univariate tests revealed that SLM, toughness, and water content were significantly higher in sun (85.21 ± 3.63 g m⁻², 125.4 ± 2.8 g, and 104.5 ± 5.3 g m⁻², respectively) than in shade (68.89 ± 2.28 g m⁻², 116.3 ± 2.9 g, and 93.3 ± 3.9 g m⁻², respectively). Leaf area did not differ in sun and shade environments. Across leaf characters and ontogenetic stages, interaction of species and leaf environment was significant (table 2). Post hoc Tukey comparisons revealed a particularly strong contrast in SLM of sun and shade leaves of *Pimenta* ($P < 0.005$).

Leaf plasticity. Species showed differences in leaf plasticity, estimated as ratios of values of sun and shade leaves (table 4). Plasticities of SLM ranged from 0.97 (*Amphitecna*) to 1.55 (*Licaria*), of leaf area from 0.8 (*Pimenta*) to 1.5 (*Eugenia*), of toughness from 0.98 (*Amphitecna*) to 1.3 (*Brosimum*), and of water content from 0.8 (*Pimenta*) to 1.71 (*Amphitecna*). Plasticities of leaf traits also differed

Table 2
Summary of MANOVA of Specific Leaf Mass, Leaf Area, Toughness, and Water Content Measured in Eight Tropical Tree Species at Los Tuxtlas, Veracruz, Mexico

Main factor	Wilks's λ	Rao's R	df ^a	P value
Species	0.01	34.2	28, 380	<0.00001
Ontogenetic stage	0.36	16.9	8, 380	<0.00001
Leaf environment	0.76	8.2	4, 380	<0.00001
Species \times ontogenetic stage	0.22	3.4	56, 380	<0.00001
Species \times leaf environment	0.54	2.5	28, 380	<0.00005
Ontogenetic stage \times leaf environment	0.88	1.6	8, 380	<0.10
Species \times ontogenetic stage \times leaf environment	0.54	1.3	56, 380	<0.09

^a Note that the degrees of freedom for MANOVA are multiplied for the number of dependent variables used, in this case, four variables.

among ontogenetic stages (table 4). However, univariate analysis across all species indicated that only adults showed lower leaf plasticity in water content (1.0) than seedlings (1.4). The multivariate interaction of species and ontogenetic stage was significant (table 4), with strong univariate confirmations for leaf plasticity of SLM ($F_{14,48} = 3.1$, $P < 0.001$), toughness ($F_{14,48} = 3.6$, $P < 0.0001$), and water content ($F_{14,48} = 4.6$, $P < 0.00001$). Toughness was different among ontogenetic stages for *Brosimum* and *Pimenta*; seedlings of *Brosimum* and juveniles of *Pimenta* showed higher plasticity in this trait (1.8 and 1.8, respectively) than conspecific juveniles (0.9) and adults (1.1), respectively. Water content was different among ontogenetic stages for *Pouteria* and *Amphitecna*; juveniles of *Pouteria* and adults of *Amphitecna* showed plasticities closer to 1 (low plasticity) in water content (1.1) than conspecific seedlings (0.43 and 3.3, respectively). Leaf plasticities were not correlated with maximum mature height.

Developmental Leaf Strategy

Mean leaf traits. MANOVA revealed that the interaction of species and ontogenetic stage was significant, indicating differences in the magnitude and direction of the ontogenetic change in mean leaf traits by species (table 2). These general and specific results are consistent with strategic responses. However, there was no correlation between species mean leaf traits and maximum mature height.

Ratios of leaf values for ontogenetic stages. Ratios of leaf area indicate different strategies for tall and short species. Ratios of early to late stages for SLM differed by maximum stature of adults. A strong negative correlation was found for the ratio of seedling to adult SLM and maximum mature height (Spearman rank correlation $r_s = -0.92$, $P < 0.001$; fig. 1a) and the ratio of seedling to juvenile SLM (Spearman rank correlation $r_s = -0.75$, $P < 0.05$; fig. 1b). The ratio of juvenile to adult SLM was not correlated with maximum mature height (Spearman rank correlation $r_s = -0.19$, $P > 0.5$; fig. 1c). The ratios of seedling to juvenile and seedling to adult SLM were greater for short species, for example, *Pouteria* (1.0 and 0.84, respectively), than for tall species, such as *Nectandra* (0.81 and 0.65, respectively). Tall species showed lower SLM as young plants than conspecific adults, while short species showed SLM ratios close to 1 at all ontogenetic stages.

Ratios of seedling to adult and seedling to juvenile leaf area were not correlated with maximum mature height (Spearman rank correlation $r_s = 0.27$, $P > 0.5$ and $r_s = -0.62$, $P > 0.09$, respectively). The ratio of juvenile to adult leaf area was strongly correlated with maximum mature height (Spearman rank correlation $r_s = 0.92$, $P < 0.005$; fig. 1d). The ratio of juvenile to adult leaf area was greater for taller species. For example, tall *Nectandra* had a higher ratio (2.1) than short *Pouteria* (0.96). Juveniles of tall species had larger leaves than conspecific adults, while short species had similar leaf areas (ratios close to 1) as juveniles and adults.

Table 3

Summary of ANOVAs on Mean Specific Leaf Mass, Leaf Area, Toughness, and Water Content (\pm SE) for Three Ontogenetic Stages of Eight Tropical Tree Species at Los Tuxtlas, Veracruz, Mexico

Leaf trait	Ontogenetic stage			$F_{2, 95}$
	Seedlings	Juveniles	Adults	
SLM (g m^{-2})	64.8 \pm 2.5 ^B	72.3 \pm 4.1 ^B	89.9 \pm 3.6 ^A	36.48*
Leaf area (cm^2)	46.4 \pm 5.2 ^A	59.9 \pm 5.6 ^B	51.5 \pm 5.1 ^A	8.18**
Toughness (g)	113.3 \pm 3.6 ^{B,C}	117.9 \pm 3.8 ^B	128.6 \pm 2.7 ^A	8.69**
Water content (g m^{-2})	79.4 \pm 5.1 ^C	97.1 \pm 6.4 ^B	116.2 \pm 4.3 ^A	23.77*

Note. Analyses were performed on log-transformed data. Different letters within a row indicate that means are significantly different with a post hoc Tukey test ($P \leq 0.05$).

* $P < 0.0001$.

** $P < 0.0005$.

Table 4

Summary of MANOVA of Leaf Plasticities of Specific Leaf Mass, Leaf Area, Toughness, and Water Content Measured in Eight Tropical Tree Species at Los Tuxtlas, Veracruz, Mexico

Main factor	Wilks's lambda	Rao's R	df	P value
Species	0.12	4.9	28, 192	<0.00001
Ontogenetic stages	0.71	2.2	8, 192	<0.05
Species × ontogenetic stage	0.10	2.6	56, 192	<0.00001

Note. Note that the degrees of freedom for MANOVA are multiplied for the number of dependent variables used, in this case, four variables.

Ratios of toughness and water content were less informative. Ratios of toughness among ontogenetic stages were not correlated with maximum mature height, nor were ratios of water content (Spearman, $P > 0.5$).

Discussion

Changes in leaf characters with ontogeny of a tree may reflect immediate responses to local light conditions or a long-term developmental strategy (Winn 1996b; Martínez-Garza 2003). Immediate responses to environment might suffice if all forest tree species encountered variable light levels in their transition from seedling to adult and all had similar capacity to adjust leaf traits to immediate environmental conditions. One would expect all leaves in sunny environments to have smaller leaf area, higher SLM and water content, and greater toughness than leaves in shade environments. In addition, all species should have similar plasticities for leaf traits; developmental leaf changes should be unrelated to maximum mature height. Because adults are more able to assimilate carbon, adults are expected to develop larger and heavier leaves than seedlings (Oberbauer and Strain 1986; Kitajima 1994), but such species-defined changes should be proportional to the size of average leaves of the species. If, in contrast, changes in leaf traits are part of a developmental strategy reflecting differences among species in the conditions met by growth to different sizes and canopy exposures, response of leaf traits to immediate environmental conditions, leaf plasticity, and developmental leaf change should be related to maximum mature height of a species. For tall species, the changes are expected to be larger than for short species. In contrast, lower leaf plasticity and less developmental leaf change are likely to be expressed in short species encountering less light variability from seedling to adult stages. The question at hand is whether leaf characters reflect immediate response, developmental strategy, or both in late-successional rain forest trees.

Mean Leaf Traits: Conditional Responses

In our study, a general analysis of all species together clearly showed expected changes in mean leaf traits as a response to prevailing sun and shade environments; leaves of plants in sun environments had lower mean leaf area, higher SLM and water content, and greater toughness than leaves of plants in shade environments. Except for the SLM of *Pimenta*, these mean responses detected in a multivariate analysis with hundreds of degrees of freedom were less obvious in

conservative pairwise tests of individual traits by species, each with fewer than 10 degrees of freedom. We suspect that horizontal and vertical heterogeneity in light levels inside the forest (Chazdon and Fetcher 1984), including short-term high light levels from sun flecks (Percy et al. 1994), temporary small canopy gaps above individuals under low light (Howe 1990), and other sources of heterogeneity over time, obscure differences for small samples of individual plants. The multivariate tests do demonstrate that average differences among sun and shade leaves are real and substantial.

Plasticities: Conditional Responses and Developmental Strategy

If plasticity ratios of sun and shade values of leaf traits reflected maximum mature height, plasticity itself could be considered an ontogenetic strategy. Because mean leaf plasticities in our study differ by species but are not correlated with maximum mature height, the plasticities implied by leaf traits that vary with environment constitute conditional responses to immediate environmental circumstances rather than developmental strategies for meeting predicted future conditions.

Similar plasticities of leaf traits at all ontogenetic stages are consistent with the observation that individual trees are intermittently overtopped and released many times before they reach mature height (Whitmore 1996). Plants respond to higher light levels at early ontogenetic stages to adjust to gap conditions and at the adult stage to cope with the environmental conditions at the top of the crown. However, once juveniles are overtopped, they need to survive under low-light conditions; in addition, adults maintain photosynthetic leaves at the bottom of their crowns in shade. Development of leaves adapted to shade environments (i.e., lower leaf mass per unit area) allows photosynthesis at low light levels. Similar plasticities of SLM, leaf area, and toughness by ontogenetic stage constitute conditional responses to immediate environmental circumstances.

One trait that does not respond to sun and shade conditions in adult leaves but does in seedlings is water content. The tallest tree on earth, *Sequoia sempervirens*, at up to 112 m, offers the example of increasing water stress with height above the ground, with extreme stress for the highest leaves in the crown (Koch et al. 2004). Measurements in *Sequoia* within the range of heights of our trees clearly show water stress with height, as do measures of water stress in spruce of more moderate size (*Picea abies*; Niinemets 1997). Both studies indicate a more general case applicable to our sample; adults may not have sufficient water available for leaves to

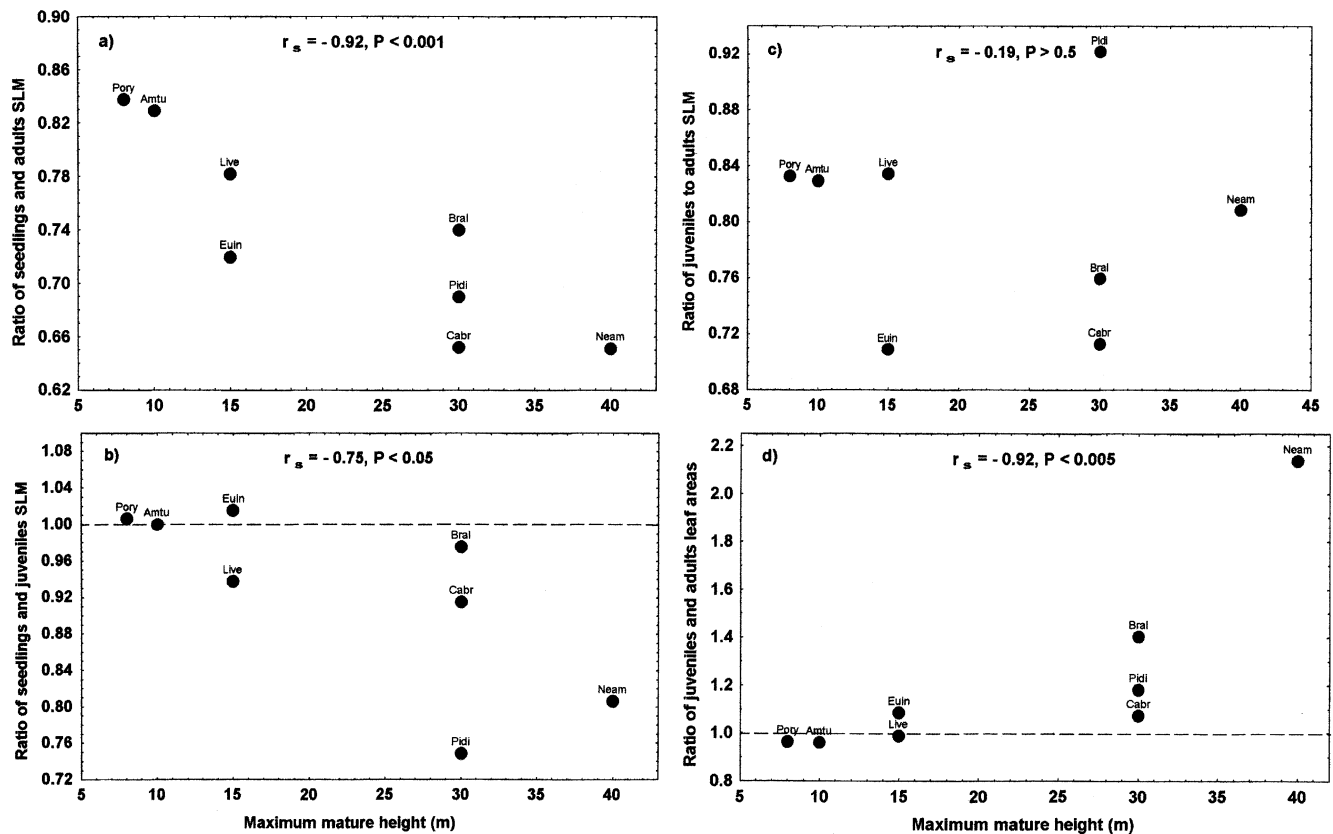


Fig. 1 Correlation between the developmental leaf change and maximum mature height of eight nonpioneer tropical tree species from Los Tuxtlas, Veracruz, Mexico. Developmental leaf change in (a) specific leaf mass (SLM) from seedlings to adults, (b) SLM from seedlings to juveniles, (c) SLM from juveniles to adults, and (d) leaf area from juveniles to adults. See table 1 for key to species names.

adjust water content to different environmental conditions, especially if availability changes over short time periods at different heights above the ground. Because leaf plasticities differ by species but are not correlated with maximum mature height, the plasticities implied by leaf traits that vary with environment constitute conditional responses to immediate environmental circumstances rather than developmental strategies for meeting predicted future conditions.

Developmental Strategy

Our results show that mean leaf traits change through ontogeny and that the magnitude and direction of change for SLM and leaf size, what we call developmental leaf change, depend on the future habitat of the species as adults. Overall, the observed ratios of seedling to adult leaf characters were 1 : 1.4 for SLM, 1 : 1.5 for water content, and 1 : 1.1 for leaf area and toughness, likely results from constraints in carbon allocation that prevent seedlings from having large and heavy leaves like adults (Oberbauer and Strain 1986; Kitajima 1994). Here the direction and degree of change in SLM and leaf area during development depended on maximum mature height, indicating developmental strategy. This result, in our case including the span of stages from seedling to juvenile to adult, is consistent with changes in leaf traits from poles to adults in Malaysian species (Thomas and Ickes 1995; Thomas

and Bazzaz 1999). In both Malaysia and Mexico, tall species show higher developmental leaf change than short species. Short species germinate and establish inside the forest; the environment they inhabit as adults is more similar to the environment that they experience as seedlings or juveniles than the habitat that tall species experience as adults. Tall species inhabit the forest understory as seedlings but occupy increasingly bright environments as they grow to maturity. Hence, leaf traits change substantially from seedling to adult to fill adult niches of tall canopy species. Those species that inhabit the understory all of their lives are less able to change leaf traits through ontogeny, reflecting what we term developmental leaf change, than those species that inhabit the canopy. Tall species show greater change in SLM and leaf area from early to late ontogenetic stages. Developmental leaf change allows tall species to endure the changes in light availability on their way to the canopy.

Only speculation is possible about contributions of phenotypic plasticity and developmental strategy to the fitness of tropical trees growing under seminatural conditions, but studies of an annual mint (*Dicerandra linearifolia*) in the southeastern United States do indicate that both conditional responses and strategy contribute to fitness (Winn 1996a, 1996b). Following Winn, we argue that environmental conditions are less predictably different in shaded understory than

in open sites where sunlight is predictable, in the first case favoring phenotypic plasticity and in the second developmental strategy. One can imagine circumstances, apparently reflected in our sample of trees from Los Tuxtlas, in which plants respond to local conditions, predictable future conditions, or both. One of us (Martínez-Garza 2003) has shown for a different set of species in a different experiment that the coefficient of variation in leaf density is related to maximum mature height in midcanopy species ($R^2 = 0.46$), but not in canopy species ($R^2 = 0.0$). An implication is that in midcanopy trees variability is built into responses to immediate conditions, whereas in tall canopy species developmental programming is more important.

Implications for Restoration

Variability in leaf traits of deep-forest species has implications for restoration and forest regeneration. Leaf plasticity and developmental leaf change may help predict which forest species perform best in habitats outside the forest and therefore are best suited for restoration projects. For instance, if different mean values or high plasticity in leaf traits are associated with high growth rates and survival in early-successional

environments, then trees with traits easily measured in many environments (Reich et al. 1999), such as high SLM or high plasticity in SLM, may prove to be better candidates for restoring forest diversity than either a random pick of forest plants or short-lived pioneers (Martínez-Garza and Howe 2003). These characteristics offer easily measured variables that may provide criteria for selection of species for planting mixed-species stands.

Acknowledgments

We thank the staff of the Los Tuxtlas Biological Station, J. Nuñez from the Institute of Ecology (Universidad Nacional Autónoma de México [UNAM]), and R. Bye from the Botanical Garden (UNAM) for their support. We are grateful to N. Cordeiro, P. Fine, J. Fornoni, N. Ingle, M. Jorge, J. Klock, S. Russo, S. Saha, A. Sullivan, and B. Zorn-Arnold for comments on the manuscript. This study was supported by the Consejo Nacional de Ciencia y Tecnología of Mexico, the Lincoln Park Zoo of Chicago (C. Martínez-Garza), and in part by the National Science Foundation of the U.S.A. (H. F. Howe).

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